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The Canadian Entomologist

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The Canadian Entomologist

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Studies on the Genus *Rhamphomyia* Meigen: A Revision of the Nearctic Species of the *basalis* Group of the Subgenus *Pararhamphomyia* Frey (Diptera: Empididae)[1]

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The group of species related to *Rhamphomyia basalis* Loew is characterized in the male by an enlarged femorotibial joint of the hind leg and usually by modifications of the femur or tibia or both, and in the female by broad, usually infuscated wings and more or less pennate legs.

The typical species belong to Frey's Group 1 of the subgenus *Pararhamphomyia* (Frey, 1955, pp. 455-457), which he characterized by the pale grey-pollinose thorax, strong uniserial dorsocentral bristles, rectangular axillary angle of the wing, open hypopygium with slender penis, and frequently pennate female legs. However, species such as *prava* and *hypsela* indicate that thoracic coloring and bristling are not good group characters but vary between very closely related species.

The *basalis* group is characterized as follows: Antenna with third joint three to four times as long as broad and more or less evenly tapering to apex. Thorax pale grey-pollinose, rarely dark brown; vittae present or absent; dorsocentrals uniserial or biserial. Axillary angle of wing rectangular. Legs usually setulose or short-bristled, rarely (*dimidiata*) long-haired; metatarsi not or only moderately swollen; hind femorotibial joint in male deformed or enlarged, the femur usually swollen and the tibia deformed; posterior legs in female usually pennate. Hypopygium with large, well-developed cercus; subcercal process evident, broad preapically, with a simple or furcate tip; tergal lobe short, directed posterodorsally, suddenly constricted preapically, with a dorsal apical cluster of stubby bristles (in a few species gradually tapering to apex with an apical group of small, slender bristles); aedeagus short and somewhat thickened (except in *arctotibia* in which it is long and whiplike).

Three European species appear to belong in this group. These are *dentipes* Zetterstedt, *intermedia* Frey, and *dentata* Oldenburg; all have genitalia very similar in general structure to those of *arctotibia*, new species.

The two Mexican species are rather distinct from the other North American species, and generally appear to be more primitive (i.e., less modified). However, they exhibit sufficient similarities in structure and bristling to be included here.

One species, *valga*, is only doubtfully included here. The form of the genitalia is rather distinct, and the modification of the femorotibial joint is very different from those of the other species. However, as association with other species groups of *Pararhamphomyia* is equally difficult, the species, because of the joint distortion, is included in this paper.

Except for the two species from Mexico, the group is restricted in North America to the northeastern portion of the continent. One species, *Rhamphomyia effera* Coquillett, described from Colorado, may belong to this group,

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[2]Associate Entomologist.

but the type is a female, and until the male is found no definite allocation of this form can be made.

Specimens from the following museums were examined: Canadian National Collection of Insects, Ottawa; U.S. National Museum, Washington, D.C.; Academy of Natural Sciences, Philadelphia, Pa.; Museum of Comparative Zoology, Cambridge, Mass.; and the Snow Entomological Museum, Lawrence, Kansas. The types of all species have been examined. I am especially grateful to Mr. G. E. Shewell, Entomology Division, Ottawa, and Mr. C. W. Sabrosky, U.S. National Museum, Washington, D.C., for allowing me to make use of their unpublished notes on types and other material of *Rhamphomyia*, and to examine homotypes selected by them as well as other valuable material in collections in their charge.

A detailed description of the *basalis* group, as a composite of the species included in this study, is as follows.

Adult

Head.—Subspherical; ocellar triangle prominent. Eye large, weakly incised next antenna; facets distinctly larger above a line drawn through incisions. Eyes contiguous above antennae in male, distinctly separated in female with two to several pairs of frontal setulae on frons; face bare, parallel-sided, slightly narrower than female frons. Basal segments of antenna subequal, setose, variable in color from yellowish-red to black; third segment three to four times as long as broad, more or less evenly tapering (Figs. 25-28) to an apical style that is one-eighth to one-half as long as third segment. Proboscis as long as vertical diameter of head; labellum fleshy. Palpus short, weakly setose, yellow or (Mexican species) black. Occipital bristles yellow to black, often forming a complete row behind the eyes; postoccipital bristles forming one to several irregular rows behind that. Ventral head bristles yellow to black.

Thorax.—From pale brownish-grey with distinct brown acrostichal and dorsocentral vittae, through unicolorous pale grey-brown, to dark greyish-brown with vittae between dorsocentral and acrostichal bristle rows. One row (rarely two rows) of pronotal bristles. Propleuron bare or setulose on median portion. Acrostichal bristles weak, irregularly biserial, ending abruptly opposite wing bases. Dorsocentral bristles uniserial, weak anteriorly, last two to four bristles distinctly stronger. One to three sublateral bristles, one posthumeral, one to three strong supraalars, one to several setulose intraalars, one strong and several weak humerals, one strong postalar, one to several setulose anterior and three (rarely two) strong posterior notopleurals. Two (rarely three or four) pairs of scutellar bristles, the apical ones distinctly stronger. Metapleural bristles numerous, usually with three to six strong ones anteriorly and several smaller weaker ones posteriorly. (A new species, *prava*, is unique in having many more thoracic bristles than described above). Squama pale yellow to brown; marginal hairs yellow to black. Haltere pale yellow, sometimes with knob infuscated. Wing in male clear or slightly infuscated; in female usually broader and shorter, slightly to heavily infuscated (clear in some European species); veins pale yellow to medium brown.

Legs.—Yellow to black; when yellow, tarsi and often much of tibiae infuscated. Fore coxa with three to 12 bristles in a row on anterior surface. Fore femur slender, usually without distinct bristles, rarely with a row of short ventral bristles. Fore tibia slender, usually with only apical bristles distinct. Fore tarsus slender with metatarsus twice as long as next segment, rarely moderately swollen and less than twice as long as next segment.

Mid coxa with an irregular double row of anterior setulae. Mid femur with anteroventral bristles short, in a regular row decreasing apicad in male, setulose or increasing apicad in female; posteroventral bristles similar but more slender in male, setulose or pennate in female; anterodorsals usually setulose, sometimes pennate in female. Mid tibia setulose or with two to five anterodorsal and posterodorsal bristles, rarely (*dimidiata*) with numerous long hairs. Mid tarsus slender and unmodified.

Hind coxa with numerous anteroventral setulae forming a weak basal tuft, with four to six strong anterodorsal bristles. Male: Hind femur slender, or swollen medially or preapically, usually with numerous anteroventral bristles clustered near the widest point, rarely with an even row of anteroventral bristles; with a posteroventral bristle row that is setulose except for a few strong bristles preapically or basally. Femorotibial joint elongate or swollen, usually rectangular in profile. Hind tibia variously modified (Figs. 1-12), often constricted medially or with a ventral ridge, in the *basalis* complex with a prebasal bristle tuft posteriorly; bristles absent except dorsally, where they vary from a few bristly hairs to numerous, long, curled bristles. Female: Hind femur slender; bristling variable from only a few preapical posteroventral bristles to full rows of strong, pennate bristles on anteroventral, anterodorsal, posterodorsal, and posteroventral surfaces; rarely (*hypsela*) with a row of ventral bristles that become stronger apicad. Femorotibial joint normal. Hind tibia slender, variable in bristling: completely setulose, with a few anterodorsal bristles, or with full rows of more or less pennate bristles on anterodorsal and posteroventral bristles. Male and Female: Hind metatarsus moderately swollen, twice as long as the next joint, completely setulose or with pennate or slender dorsal and anterodorsal bristles.

Abdomen.—Lightly pollinose, yellow to brownish-black in ground color; venter often paler. Bristling variable from black to pale yellow. Male hypopygium as described in the diagnosis. Female ovipositor elongate, not heavily sclerotized; cercus six to eight times as long as broad, weakly haired.

Life-History and Habits

Three of the twelve species have been reared from dead wood (usually old stumps) and the other species probably have the same larval habitat. Malloch (1917) described the larva and pupa of *dimidiata*, but the virtual absence of descriptions of the immature stages of other species of *Rhamphomyia* makes it impossible to draw any conclusions concerning the diagnostic characters of the group.

Adults have usually been collected only in small numbers by sweeping. Some species at least are attracted to light, especially during rainy weather. Otherwise there is no information on adult habits.

Key to Nearctic Males of *Pararhamphomyia basalis* group

1. Hind tibia bearing crest of flattened bristles anteriorly near base; hind femur wider preapically 2
   Hind tibia without such a crest, hind femur of even width throughout or wider at or before middle 5
2. Dorsocentral bristles biserial; propleural hairs present; dark-brown species ..... *prava* n. sp.
   Dorsocentral bristles uniserial; propleural hairs absent; pale-grey species 3
3. Hind tibia not arcuate; basal crest one-fifth as long as tibia; hind femur with anteroventral bristles not crowded towards apex ..... *basalis* Loew
   Hind tibia arcuate, basal crest well-developed, more than one-fourth as long as tibia; hind femur with anteroventral bristles clumped preapically 4
4. Hind tibia strongly arcuate, with many long dorsal bristles basad; with only a few strong, ventral bristles on basal third ..... *clauda* Coquillett

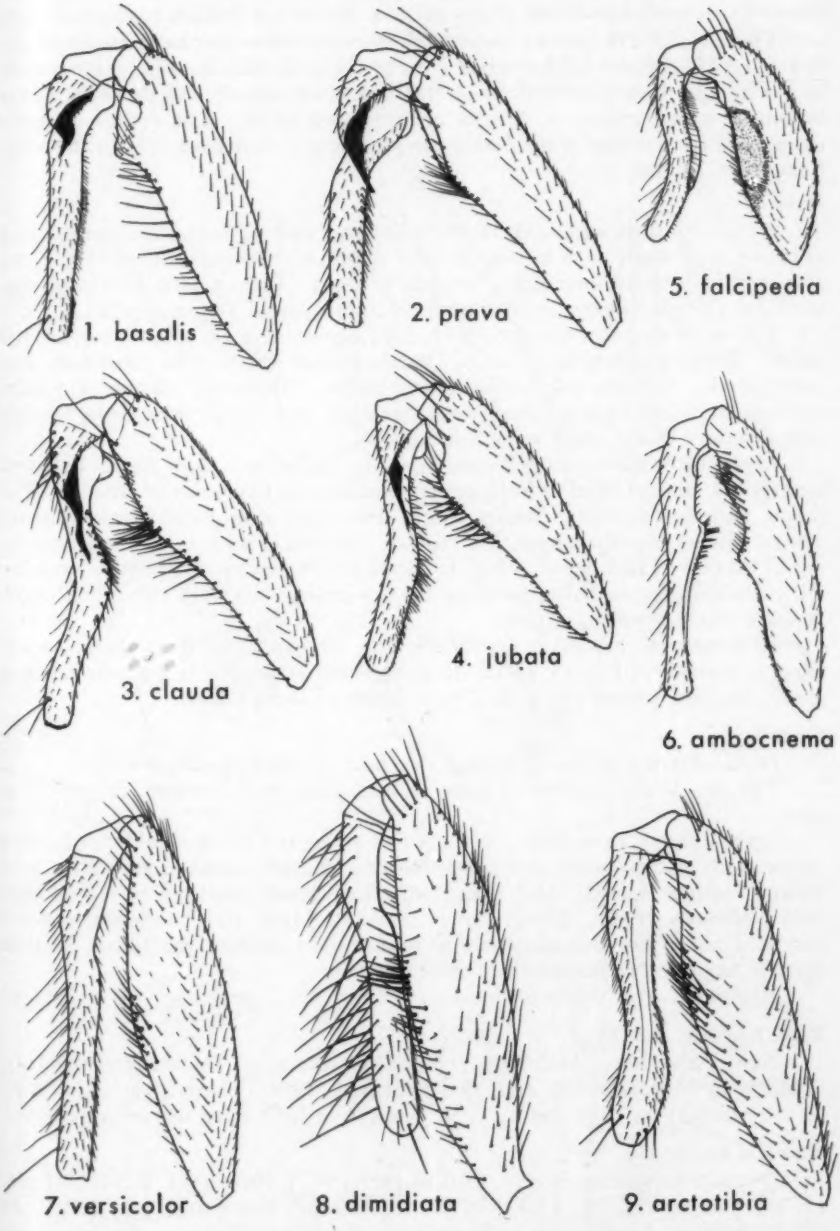
Hind tibia only slightly arcuate, with only a few weak dorsal bristles basad; with many short, strong, ventral bristles on median half ..... *jubata* n. sp.

5. Middle portion of hind tibia strongly compressed laterally; propleuron haired (except in *hypsela*) 6
Middle portion of hind tibia tubular or slightly compressed dorsoventrally; propleuron bare 10
6. Hind femur with ventral bristles sparse medially, femur of equal width throughout (Mexican species) 7
Hind femur with ventral bristles strongest medially, femur medially swollen 8
7. Propleuron haired; numerous strong ventral bristles on hind femur ..... *tolucensis* n. sp.
Propleuron bare; ventral bristles on hind femur in an even row, not unusually strong ..... *hypsela* n. sp.
8. Hind tibia flattened and constricted only briefly on median portion, with no strong dorsal bristles except preapically; abdomen dark ..... *arctotibia* n. sp.
Hind tibia strongly flattened and bladelike for most of its length, with long dorsal bristles; abdomen yellow 9
9. Hind tibia with numerous, very long dorsal bristles; mid tibia covered with long hairs and bristles ..... *dimidiata* Loew
Hind tibia with only six to eight long dorsal bristles; mid tibia with only short hairs ..... *versicolor* n. sp.
10. Hind femur with a broad, flat, pubescent area anteroventrally with no strong bristles ventrally ..... *falcipedia* n. sp.
Hind femur with no such flattened area, but with strong ventral bristles 11
11. Hind tibia with basal articulation strongly swollen and circular in profile, without a median anteroventral ridge ..... *valga* Coquillett
Hind tibia with basal articulation not strikingly enlarged, rectangular in profile, medially with a glossy anteroventral ridge ..... *ambocnema* n. sp.

Key to Nearctic Females of *Pararhamphomyia basalis* group

1. Abdomen and thoracic humeri yellow 2
Abdomen and thoracic humeri dark 3
2. Hind femur posteroventrally pennate ..... *versicolor* n. sp.
Hind femur not pennate ..... *dimidiata* Loew
3. Femur and tibia of both middle and hind legs distinctly pennate; hind metatarsus dorsally pennate ..... *valga* Coquillett
At least mid tibia and hind metatarsus setulose or bristled 4
4. Dorsocentral bristles biserial; propleuron medially setulose ..... (?)[3] *prava* n. sp.
Dorsocentral bristles uniserial; propleuron setulose or bare 5
5. Thorax with more or less distinct brown vittae along dorsocentral and acrostichal rows 6
Thorax without distinct brown vittae, but with a pair of dark vittae, visible in anterior view, between bristle rows 11
6. Propleuron medially setulose; six scutellar bristles; mesonotal bristles numerous ..... *arctotibia* n. sp.
Propleuron bare medially; four scutellar bristles; mesonotal bristles sparse 7
7. Abdominal hairs yellow; thoracic setulae brownish 8
Abdominal hairs dark; thoracic setulae black 9
8. Style two-fifths as long as third antennal segment; thorax with several humeral bristles and two supraalar bristles ..... *ambocnema* n. sp.
Style one-fourth as long as third antennal segment; thorax with only two or three humeral bristles and one supraalar bristle ..... (?) *falcipedia* n. sp.
9. Base of wing whitish-hyaline, contrasting with infuscated discal area; mid femur without pennate setule ..... *basalis* Loew
Base of wing infuscated, concolorous with apical portion; mid femur posteroventrally pennate 10
10. Style only about one-seventh as long as third antennal segment (Fig. 25) ..... *jubata* n. sp.
Style approximately one-fourth as long as third antennal segment (Fig. 26) ..... *clauda* Coquillett
11. Propleuron medially haired; hind femur distinctly pennate; mid tibia without distinct bristles ..... *tolucensis* n. sp.
Propleuron medially bare; hind femur not distinctly pennate; mid tibia with numerous bristles ..... *hypsela* n. sp.

[3]Females not yet known; key characters hypothesized.



Figs. 1-9. *Rhamphomyia* (*Pararhamphomyia*) spp. Right hind femora and tibiae, anterior views.

Rhamphomyia (Pararhamphomyia) basalis Loew

Figs. 1, 13, 27

Rhamphomyia basalis Loew, 1864, p. 77; Coquillett, 1895, p. 410; Melander, 1925, p. 187.

The male of this species shares with the next three species the apically enlarged hind femur and basal anterior crest of the hind tibia, but differs from them in having the hind tibia straight on the apical two-thirds and the hind femur lacking a strong clump of bristles at its widest point. The female is easily recognized from others of the *basalis* complex by the clear basal cells of the wing. Length 4.5-5.5 mm.

Male

Head.—Antenna with basal joints yellowish; third segment four times as long as broad; style one-fourth as long as third segment. Occipital bristles black, the row usually broadly interrupted on side of head. Postoccipital bristles strong, black, in a single, usually regular row. Ventral bristles long and pale.

Thorax.—Pale brownish-grey with faint brown acrostichal and dorsocentral vittae. Propleuron medially bare. One sublateral bristle, two supraalars, two notopleurals. Squama pale yellow with yellow hair-fringe. Knob of haltere or three intraalars, two or three weak humerals, and one or two weak anterior pale yellow. Wing clear; veins pale yellow.

Legs.—Yellowish basad; femora apically infuscated, and tibiae and tarsi entirely so; bristles black. Fore coxa with three to five anterior bristles. Mid femur with anteroventral bristles short, alternately strong and weak; posteroventral bristles slightly longer, less regular. Mid tibia with two median anterodorsal bristles. Hind leg as in Fig. 1; femur with anteroventral bristles irregular, distinctly stronger medially; posterior bristles stronger on basal third; hind metatarsus scarcely swollen, setulose.

Abdomen.—Brownish in ground color; venter pale; hairs dark brown. Hypopygium as in Fig. 13; cercus helmet-shaped in profile; tergal lobe tapering evenly to apex, preapically with a ventral tuft of short bristles.

Female

Head.—Frons pearl-grey, bearing two pairs of small frontal bristles.

Thorax.—Wings hyaline to apex of basal cells, then strongly infuscated to apex.

Legs.—Paler than in male, only apex of tibiae and all tarsi infuscated. Mid femur with anteroventral and posteroventral surfaces setulose, the latter with stronger setulae apicad. Mid tibia with anterodorsal bristles scarcely stronger than adjacent setulae. Hind femur setulose. Hind tibia with anterodorsal and basal half of posteroventral row of setulae short pennate, the flattened setulae equal in length to, or shorter than, tibial diameter.

Abdomen.—Pale yellowish-brown.

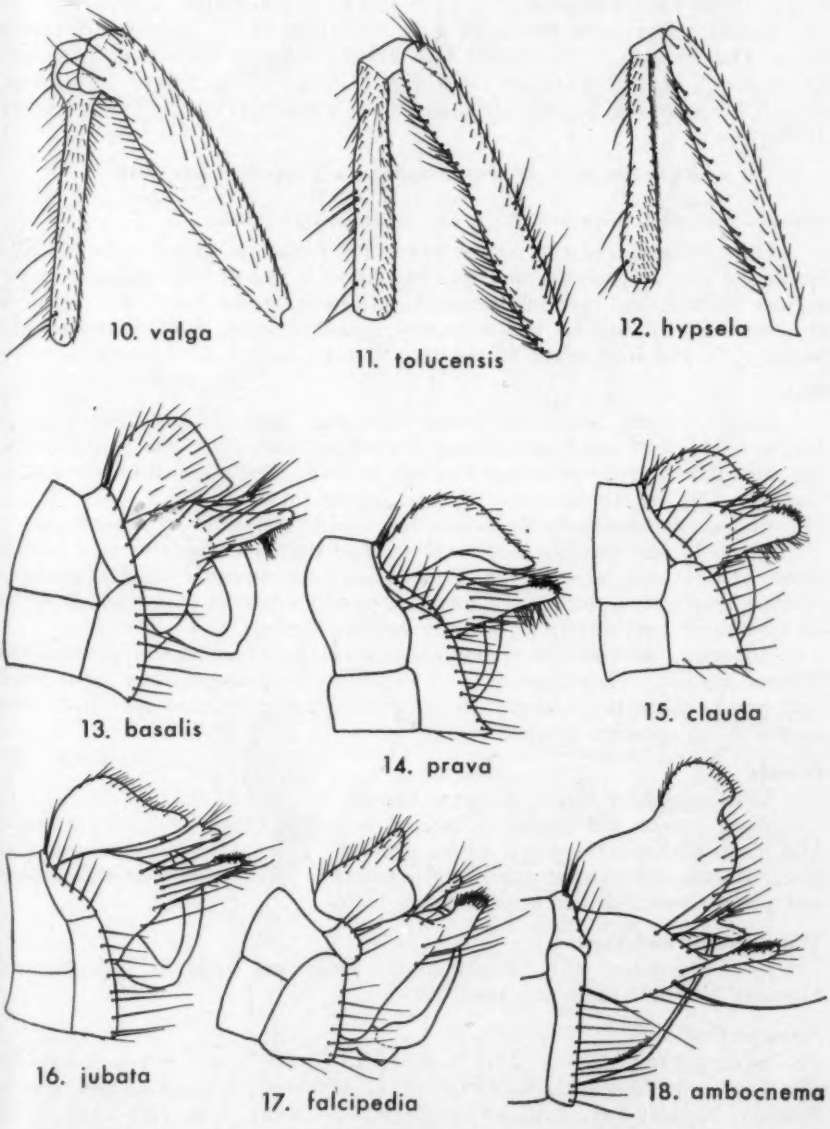
Type Locality and Type

New Hampshire. Holotype, female, in Museum of Comparative Zoology, Cambridge, Massachusetts; examined February, 1959. Homotypes selected by C. W. Sabrosky in 1950, and by G. E. Shewell in 1953, have also been examined.

Material Examined 16 ♂♂, 53 ♀♀.

QUEBEC. Kazabazua, 3 ♂♂, 6-10.VI.1927 (W. J. Brown), 1 ♀, 7-10.VI.1927 (J. McDunnough), 1 ♀, 6.VI.1956 (W. R. Mason); Knowlton, 1 ♀, 12.VI.1928 (J. A. Adams); Laniel, 1 ♀, 6.VI.1938 (C. E. Atwood), 1 ♀, 14.VI.1942 (O. Peck), 1 ♂, 17.VIII.1935 (H. S. Fleming), 1 ♀, 9.VI.1939 (F. P. Ide), 1 ♀, 14.VI.1939 (F. P. Ide) (homotype); Maniwaki, 1 ♂, 28.VI.1925 (C. H. Curran); Wakefield, 1 ♀, 26.VI.1946 (G. E. Shewell); Lac Mondor, Ste. Flore, 3 ♂♂,

13 ♀♀, 27.V.1951 (E. G. Munroe), 1 ♀, 3.VI.1951 (E. G. Munroe), 1 ♀, 28.VI.1951 (E. G. Munroe); Cascapedia River, 1 ♀, 21.VII.1933 (W. A. Reeks); Baie Comeau, 1 ♀, 1.VII.1948 (E. G. Munroe); Mt. Albert, 1 ♀, 24.VII.1954 (J. E. H. Martin). ONTARIO. Honey Harbor, 1 ♂, 2.VI.1932 (G. S. Walley); Low Bush, Lake Abitibi, 1 ♂, 1 ♀, 25.VI.1925 (N. K. Bigelow), 2 ♀♀, 17.VI.1925 (N. K. Bigelow), 1 ♀, 6.VII.1925 (N. K. Bigelow), 1 ♀, 30.VII.1925



Figs. 10-18. *Rhamphomyia* (*Pararhamphomyia*) spp. 10-12, right hind femora and tibiae, anterior views; 13-18, male hypopygia, left lateral views.

(N. K. Bigelow); Simcoe, 1 ♀, 28.V.1938 (G. E. Shewell); Kearney, 2 ♀♀, 22-23.VI.1926 (F. P. Ide); Orillia, 1 ♀, 10.VI.1925 (C. H. Curran). LABRADOR. Goose Bay, 1 ♀, 2.VII.1948 (W. E. Beckel). NOVA SCOTIA. Baddeck, 1 ♀, 2.VII.1936 (T. N. Freeman). MAINE. Bar Harbor, 1 ♀, 7.VI.1921 (C. W. Johnson); Echo Lake, Mount Desert, 1 ♀, 12.VII.1918 (C. W. Johnson); Round Pond Mountain, 1 ♀, 29.VII . NEW HAMPSHIRE. Franconia, 1 ♀ (Mrs. Slosson); Pinkham, N., 1 ♂, 6.VII. (N. Banks); White Mountains, 4 ♂♂, 6 ♀♀ (Morrison); Randolph, 2 ♀♀, 25-30.VI. (N. Banks), 1 ♀, 2.VII. (N. Banks). MARYLAND. Baltimore, 1 ♂, 16.V.1938 (E. G. Fisher). PENNSYLVANIA. Hazelton, 1 ♀, 26.VI.1913 (Dr. Dietz). NORTH CAROLINA. Clingman's Dome, 1 ♀, 13.V.1956 (reared from dead wood) (W. E. Snow). MICHIGAN. Clear Lake near Big Rapids, Mecosta Co., 1 ♀, 4.VI.1938 (C. W. Sabrosky) (homotype).

Rhamphomyia (*Pararhamphomyia*) *clauda* Coquillett

Figs. 1, 13, 27

Rhamphomyia clauda Coquillett, 1901, p. 601; Melander, 1925, p. 188.

This species shares with *basalis*, *prava*, and *jubata* the greatly enlarged hind femur and basal crest on the hind tibia, but differs in that the hind tibia is strongly arcuate inwards, and bears numerous dorsal bristles at the base. The female is separated from *basalis* by the uniformly darkened wing, from *jubata* by the longer style, and from *prava* by the grey thorax. Length 4.0-5.0 mm.

Male

Head.—Antenna with basal joints infuscated; third segment four times as long as broad; style one-fourth as long as third segment. Occipital bristles black, the row not or scarcely interrupted on side of head. Postoccipital bristles strong, black, in a single, regular row. Ventral bristles short and black.

Thorax.—As described for *basalis*, but bristles generally slightly stronger.

Legs.—As described for *basalis* except: mid tibia with three or four anterodorsal bristles; hind leg as in Fig. 3; femur with anteroventral bristles forming a strong clump at two-thirds from base, the posterior bristles strong and irregular on basal third; hind metatarsus scarcely swollen, setulose.

Abdomen.—Brownish in ground color; venter pale basally, concolorous with dorsum apically. Hypopygium as in Fig. 15; cercus longer than high; tergal lobe narrowed sharply medially, then parallel-sided to rounded apex, apex with several short, spinelike bristles.

Female

As described for *basalis*, except as follows.

Wing evenly and deeply infuscated to base. Thoracic bristles stronger. Mid femur with posteroventral setulae pennate. Hind femur with anterodorsal, posterodorsal, and posteroventral setulae pennate. Hind tibia with anterodorsal and posteroventral setulae pennate throughout.

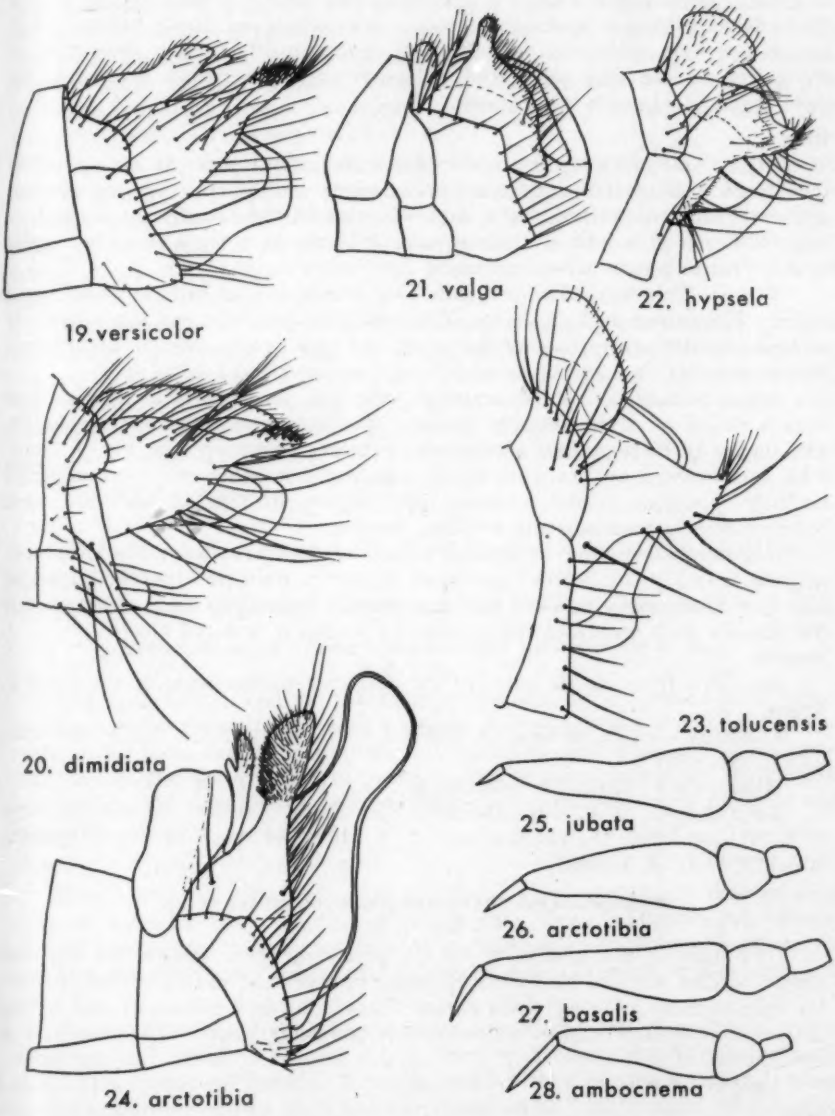
Type Locality and Type

New Hampshire (Mt. Washington). Holotype, male, in U.S. National Museum, No. 5492, examined April, 1958.

Material Examined 31 ♂♂, 39 ♀♀.

QUEBEC. Laniel, 11 ♂♂, 13 ♀♀, 4-18.VI.1939 (F. P. Ide), 4 ♀♀, 7.VII.1939 (F. P. Ide), 1 ♂, 2 ♀♀, 4.VI.1939 (J. L. Hitchon), 1 ♀, 8.VI.1941 (A. R. Brooks); Norway Bay, 1 ♀, 2.VI.1938 (E. G. Lester), 1 ♀, 30.V.1938 (E. G. Lester); Kazabazua, 2 ♀♀, 6.VI.1956 (W. R. M. Mason), 1 ♀, 28.V.1933 (G. S. Walley); Harrington Lake, Gatineau Park, 1 ♂, 27.V.1954 (R. McCondochie),

1 ♀, 27.V.1954 (H. J. Huckel), 1 ♀, 2.VI.1954 (R. McCondochie); Lac Mondor, Ste. Flore, 9 ♂♂, 5 ♀♀, 20.V.-27.VI.1951 (E. G. Munroe), ONTARIO. 1 ♀ (no data). NEW BRUNSWICK. Fredericton, 1 ♂, 1 ♀, 14.V.1921. NOVA SCOTIA. Kentville, 1 ♂, 1 ♀, 3.VI.1924 (R. P. Gorham), 1 ♂, 18.VI.1924 (R. P. Gorham); Annapolis, 1 ♀, 21.VI.1924 (R. P. Gorham). MASSACHUSETTS. Tyngsboro, 1 ♀, 31.V.1923 (H. C. Fall). NEW HAMPSHIRE. Mt. Washington, 2 ♂♂, 1 ♀ (Mrs.



Figs. 19-26. *Rhamphomyia* (*Pararhamphomyia*) spp. 19-24, male hypopygia, left lateral views; 25-28, left antennae, lateral views.

Slosson); Franconia, 1 ♂ (Mrs. Slosson); Jaffrey, 1 ♀, 18.VI. . NEW YORK. Ithaca, 1 ♀, 12.V.1936 (J. W. H. Rehn). MARYLAND. Frederick Watershed, Frederick Co., 2 ♀♀, 30.V.1939 (E. G. Fisher). NEW JERSEY. Clementon, 1 ♂ (cotype); Lahaway, Ocean Co., 1 ♀ (J. Bequaert).

Rhamphomyia (Pararhamphomyia) jubata n. sp.

Figs. 4, 16, 25

This species differs from the preceding two closely related species in that the male hind tibia is moderately arcuate without strong dorsal bristles basad, but with a long multiserial row of short ventral bristles. Both sexes may be recognized by the very short style, which is only one-seventh as long as the third segment. Length 4.0-4.5 mm.

Male

Head.—Antenna with basal joints infuscated; third segment approximately four times as long as broad; style approximately one-seventh as long as third segment. Occipital bristles black, the row more or less broadly interrupted on sides of head. Postoccipital bristles strong, black, in a single, usually regular row. Ventral bristles short and black.

Thorax.—Pale brownish-grey with faint brown acrostichal and dorsocentral vittae. Propleuron medially bare. Two sublateral bristles, three supraalars, one to two intraalars, three to four humerals, and two strong anterior notopleurals usually present. Squama, haltere, and wing as described for *basalis*.

Legs.—Infuscated, not or scarcely yellowish basad; bristles black. Fore coxa with six or seven anterior bristles. Mid femur as described for *basalis*. Mid tibia with three or four anterodorsal bristles. Hind leg as in Fig. 3; femur with anteroventral bristles weak basally, distinctly stronger and more crowded medially; posterior bristles uniserial, only slightly stronger at one-third from base; hind metatarsus scarcely swollen, setulose.

Abdomen.—Brownish in ground color; venter dark; hairs black. Hypopygium as in Fig. 16; cercus cap-shaped, distinctly narrowed preapically; tergal lobe narrowed rapidly on basal half, then weakly tapering to apex; apical portion flat dorsally with numerous short spine-like bristles in a dorsal cluster.

Female

Separable from *clauda* only by the distinctly shorter style of the antenna.

Types

Holotype.—♂, Parke Reserve, Quebec, 5.VII.1957 at light, (G. E. Shewell). C.N.C. No. 6703.

Allotype.—♀, same data as holotype.

Paratypes.—2 ♂♂, Lac Mondor, Ste. Flore, Quebec, 15.VII.1951 and 27.V.1951, at light, (E. G. Munroe); 1 ♀, 36 miles south of Clova, Quebec, 30.VI.1956 (L. A. Lyons).

Rhamphomyia (Pararhamphomyia) prava n. sp.

Figs. 2, 14

The male of this species, as for the preceding three species, has the hind femur swollen and the hind tibia crested. However, it differs strikingly from the other species in being much darker (brownish-black pollinose) and having biserial dorsocentral bristles and numerous propleural hairs. The female is as yet unknown.

Length 5.5 mm.

Male

Head.—Antenna with basal joints infuscated; third segment approximately four times as long as broad; style one-sixth as long as third segment. Occipital

bristles black, the row not interrupted laterally. Postoccipital bristles strong, black, numerous, irregularly placed, becoming hairlike ventrally.

Thorax.—Dark greyish-brown with three faint darker-brown vittae along bristle rows. Pronotal bristle row somewhat doubled laterally. Propleuron medially with about six setulae. Dorsocentral bristles presuturally not separated from numerous scattered setulose bristles; postsuturally irregularly biserial, the last six distinctly stronger. Presutural bristles numerous and undifferentiated, with one sublateral distinctly stronger. About eight subequal setulose anterior notopleural bristles. Approximately nine intraalar and supraalar bristles with one supraalar stronger; one strong and three to four setulose postalar bristles. Four to eight scutellar bristles. Metapleural bristles numerous. Squama pale yellowish-brown with black hair-fringe. Haltere dark yellowish-brown. Wing moderately infuscated; veins dark brown.

Legs.—Black, knees yellowish; bristles black. Fore coxa with ten to twelve anterior bristles. Mid femur as described for *basalis*. Mid tibia with three or four strong anterodorsal bristles above preapical one, and one weak dorsal bristle. Hind leg as in Fig. 2; femur with anteroventral bristles irregular, forming a strong clump at two-thirds from base, posterior bristles strong and biserial on basal third; hind metatarsus scarcely swollen, setulose.

Abdomen.—Black, dark brown pollinose; venter grey pollinose; bristles black. Hypopygium as in Fig. 14; cercus more slender than in the preceding species, concave on ventral margin; tergal lobe narrowed rapidly on basal half, then parallel-sided to rounded apex, apical portion rounded dorsally with numerous short spine-like bristles in a dorsal cluster.

Female

Not as yet recognized.

Types

Holotype.— ♂, Lac Mondor, Ste. Flore, Quebec, 27.V.1951 (E. G. Munroe). C.N.C. No. 6702.

Paratype.— ♂, Randolph, New Hampshire, 2.VII. (N. Banks). M.C.Z.

***Rhamphomyia (Pararhamphomyia) ambocnema* n. sp.**

Figs. 6, 18, 28

The males of this and the following species can be recognized from others in the group by the dark abdomen with pale yellow bristling and by the glossy ridge on the inner surface of the otherwise pollinose hind tibia; and *ambocnema* itself can be distinguished by the greatly enlarged cercus and relatively straight hind tibia. The female may be recognized by the yellow-haired abdomen and long style. Length 4.0-4.5 mm.

Male

Head.—Antenna with basal joints infuscated; third segment 3½ times as long as broad; style two-fifths as long as third segment. Occipital bristles pale yellow, the row more or less broadly interrupted on sides of head. Postoccipital bristles strong, pale yellow, in a single, usually regular row. Ventral bristles long and pale.

Thorax.—Medium greyish-brown, with acrostichal and dorsocentral vittae indistinct. All thoracic bristles pale yellow to brown. Propleuron medially bare. One sublateral bristle, three supraalars, two intraalars, several weak humerals, and one or two weak anterior notopleurals. Metapleural bristles very long and slender. Squama pale yellow with yellow hair-fringe. Knob of haltere pale yellow. Wing clear; veins brown.

Legs.—Evenly infuscated, only the knees pale; all bristles and hairs yellow. Fore coxa with five to seven anterior bristles. Mid femur with very short and stubby anteroventral bristles; posteroventral bristles short, alternating with weaker bristles basad, long and regular on the apical half, longest just beyond the middle. Mid tibia with three strong anterodorsal bristles above the preapical bristles. Hind leg as in Fig. 6; femur ventrally with a velvety mat of fine pubescence on basal half, a multiserial row of short anteroventral bristles on apical half, posterior row setulose; hind tibia with a series of short strong anteroventral bristles on the median crest; hind metatarsus not swollen.

Abdomen.—Brownish in ground color; venter evenly infuscated; hairs pale yellow. Hypopygium as in Fig. 18; cercus greatly enlarged, distinctly constricted preapically; tergal lobe slender, constricted medially, then slightly expanded to apex, apical portion dorsally with numerous short spine-like bristles.

Female

Head.—Frons pearl-grey, bearing one pair or no frontal setulae.

Thorax.—Wing only slightly infuscated basad, becoming moderately infuscated beyond the apex of the basal cells. Thoracic bristles darker than in the male.

Legs.—Color as in the male. Mid femur with anteroventral surfaces setulose, two widely spaced, small setulae on basal half of anteroventral surface. Mid tibia with two anteroventral, two anterodorsal, and two posteroventral bristles. Hind femur setulose except for slightly stronger bristles preapically on anteroventral and posteroventral surfaces. Hind tibia with one distinct anterodorsal and a row of short dorsal bristles.

Abdomen.—Color as in the male, the yellow hairs shorter and more prostrate.

Types

Holotype.— ♂, 5 mi. S.W. of Shilo, Manitoba, 28.V.1958 (J. F. McAlpine). C.N.C. No. 6704.

Allotype.— ♀, same data as above.

Paratypes.—2 ♂♂, 1 ♀, same data as above (swept ex *Equisetum* sp.). 1 ♂, 2 ♀♀, Ninette, Manitoba, 21.V.1958 (J. F. McAlpine) (under overhanging bank in bur oak community); 1 ♂, Aweme, Manitoba, 5.VI.1923 (R. M. White); 1 ♂, Marmora, Ontario, 23.V.1952 (J. R. McGillis); 3 ♂♂, Old Chelsea, Quebec, 27.V.1952 (C. D. F. Miller); 1 ♀, Kazabazua, Quebec, 6.VI.1956 (W. R. M. Mason); 1 ♂, Ithaca, New York, May (C. W. Johnson coll'n.).

***Rhamphomyia (Pararhamphomyia) falcipedia* n. sp.**

Figs. 5, 17

The species is very similar to the preceding, but can easily be recognized in the male by the swollen and ventrally flattened hind femur and arcuate hind tibia. The female is as yet unknown. Length 3.8-4.0 mm.

Male

Head.—Antenna with basal segments infuscated, third segment 3½ times as long as broad, style one-fourth as long as third segment. Occipital bristles yellow, the row not or scarcely interrupted on sides of head. Postoccipital bristles strong, yellow, in a single regular row. Ventral bristles long and pale.

Thorax.—As described for *ambocnema*, except: only two supraalar bristles, one weak intraalar, two or three weak humerals, and one notopleural.

Legs.—Evenly infuscated, only the knees pale; all bristles and hairs yellow or pale brown. Fore coxa with five to seven anterior bristles. Fore metatarsus slightly swollen, long-haired. Mid femur with three or four long anteroventral and three to five short stubby posteroventral bristles basad, only short setulose

bristles apicad. Mid tibia with two or three strong anterodorsal and two strong and several weak posteroventral bristles. Hind leg as in Fig. 5; femur very thick, flattened anteroventrally; anteroventral bristles altered to a multiserial row of stubby setulae around the depression; posteroventral bristles slightly longer, similarly disposed, but with a preapical comb of six to seven stubby bristles; hind tibia strongly deformed and arcuate with a polished and rounded elongate crest ventrally; hind metatarsus not swollen.

Abdomen.—Brownish in ground color; venter evenly infuscated; hairs pale yellow. Hypopygium as in Fig. 17; cercus moderate in size, with a rounded notch on posterior surface; tergal lobe strongly tapered on basal half, apical half distinctly turned upwards, apical portion dorsally with numerous short spine-like bristles.

Female

Not as yet recognized.

Types

Holotype.— ♂, Aylmer, Quebec, 28.V.1926 (C. H. Curran). C.N.C. No. 6705.

Paratype.— ♂, 13 miles north of Lapeer, Michigan, 31.V.1937 (C. W. Sabrosky).

***Rhamphomyia (Pararhamphomyia) versicolor* n. sp.**

Figs. 7, 19

This species, with *dimidiata*, is easily recognized in both sexes by the yellow thoracic humeri and abdomen. Additional characters are the sparse black bristling and distinctly vittate thorax. The male can be recognized by the very compressed hind tibiae. It differs from *dimidiata* in the male by the setulose or sparsely bristled tibiae and in the female by the pennate hind femur. Length 4.8-5.0 mm.

Male

Head.—Antenna with basal joints somewhat infuscated; third segment four times as long as broad; style one-third as long as third segment. Occipital bristles black, the row usually broadly interrupted on sides of head. Postoccipital bristles strong, black, in a single, usually regular row. Ventral bristles slender, black.

Thorax.—Pale brownish-grey, with distinct dark brown acrostichal and dorsocentral vittae. Humeri, and metapleuron around bristles, yellowish. Propleuron medially with one or two setulae. One sublateral bristle, two or three supraalars, one or two weak intraalars, six to eight weak humerals, and two weak anterior notopleurals. Squama pale yellow with brown to black hair-fringe. Knob of haltere pale yellow. Wing veins brown.

Legs.—Coxae and femora yellow; tibiae somewhat infuscated; tarsi black; bristles pale yellow. Fore coxa with six to eight anterior bristles. Fore tarsus with the basal segments somewhat swollen. Mid femur with anteroventral bristles short, strong, not distinctly alternating; posteroventral bristles weak and irregular. Mid tibia with three weak posterodorsal bristles. Hind leg as in Fig. 7; femur with anteroventral bristles forming a loose irregular median cluster of short bristles, posterior bristles only distinct basally; hind metatarsus scarcely swollen, setulose.

Abdomen.—Yellow, faintly whitish pollinose; bristles black dorsally, yellow ventrally and on hypopygium. Hypopygium as in Fig. 19; cercus slender and elongate; tergal lobe evenly tapering except for a slight constriction beyond the middle, apical portion dorsally with numerous spine-like bristles.

Female

Head.—Frons pearl-grey, bearing several pairs of small frontal bristles.

Thorax.—Wing as in the male.

Legs.—Color as in the male. Mid femur with anteroventral and posteroventral surfaces setulose, the latter with stronger setulae apicad. Mid tibia with two or three anterodorsal and two to five posterodorsal bristles. Hind femur with anterodorsal setulae weakly and posteroventral setulae strongly pennate. Hind tibia without distinct bristles or pennate setulae.

Abdomen.—Color as in the male.

Types

Holotype.— ♂, Lac Mondor, Ste. Flore, Quebec, 21.V.1951 (E. G. Munroe). C.N.C. No. 6835.

Allotype.— ♀, same locality and collector, 18.V.1951.

Paratypes.—1 ♂, same locality and collector, 30.V.1951; 1 ♀, Guelph, Ontario, 10.VI.1913 (C. H. Curran); 1 ♂, 1 ♀, Franconia, New Hampshire (Mrs. Slosson); 1 ♂, Ithaca, New York, May (C. W. Johnson).

Rhamphomyia (Pararhamphomyia) dimidiata Loew

Figs. 8, 20

Rhamphomyia dimidiata Loew, 1861, p. 325; Coquillett, 1895, p. 412; Malloch, 1917, p. 401 (larva and pupa); Melander, 1925, p. 190.

This species is very close to the preceding species, but differs in that the middle and hind legs of the male bear numerous long hair-like bristles, and the hind femur of the female bears no pennate setulae. Length 4.8-5.0 mm.

Male

Head.—As described for *versicolor*, except that the occipital row is not or scarcely discontinued laterally.

Thorax.—Dark greyish-brown, the vittae only weakly marked. Otherwise as described for *versicolor*.

Legs.—Color and fore legs as described for *versicolor*. Mid femur with numerous long fine yellow hairs on anteroventral and anterior surfaces, otherwise bristled as in *versicolor*. Mid tibia with numerous long hairs on all but posterior surfaces, a few stronger posterodorsally and posteroventrally. Mid tibia with long hairs on anterior and dorsal surfaces of two basal segments. Hind leg as in Fig. 8; femur differing from *versicolor* only in having longer bristles and setulae; hind tibia with numerous long dorsal and anterodorsal hair-like bristles; hind metatarsus scarcely swollen, distinctly long-haired.

Abdomen.—As described for *versicolor*, except: bristling much longer; hypopygium as in Fig. 20; tergal lobe more attenuate apically with fewer bristles in the apical dorsal patch.

Female

Very similar to the female of *versicolor*, but hind femur without distinct pennate setulae, only a few preapical posteroventral bristles strong and slightly flattened.

Type locality and type

Maryland. Holotype, male, in Museum of Comparative Zoology, Cambridge, Massachusetts; examined February, 1959.

Material examined 2 ♂♂, 1 ♀.

Massachusetts. no locality, 2 ♂♂ (Loew) (including holotype). Maryland. Gunpowder River, Baltimore Co., 1 ♂, 7.V.1940 (E. G. Fisher); Middle River Neck, Baltimore Co., 1 ♀, 7.V.1939 (E. G. Fisher).

***Rhamphomyia (Pararhamphomyia) arctotibia* n. sp.**

Figs. 9, 24, 26

This species can be easily recognized in the male by the hind tibia, which is strikingly narrowed just beyond the middle, then enlarged again to form a swollen apical portion. In both sexes it may be recognized by the distinctly vittate thorax and numerous thoracic bristles. Length 4.8-5.2 mm.

Male

Head.—Antenna (Fig. 26) with basal segments reddish-brown; third segment three times as long as wide; style one-fourth as long as third segment. Occipital bristles black, the row not or scarcely interrupted on sides of head. Postoccipital bristles strong, black, in a single, usually regular row. Ventral bristles long and black.

Thorax.—Pale brownish-grey with distinct brown acrostichal and dorsocentral vittae. Propleuron medially with three or four small bristles. Notal bristles numerous, a full row (sublaterals) connecting the anterior dorsocentral with the posthumeral bristle. Three supraalar bristles, two intraalars, six or seven weak humerals, and two strong and a few weak anterior notopleurals. Six scutellar bristles, outer pair weak. Squama pale yellow with brown hair-fringe. Knob of haltere yellow, stalk brown. Wing faintly infuscated along veins; veins brown.

Legs.—Entirely infuscated, knees paler; bristles black. Fore coxa with ten to twelve anterior bristles. Fore femur with three or four preapical anteroventral and a row of long slender posteroventral bristles. Fore tibia with one anterodorsal and one dorsal bristle medially. Mid femur with anteroventral bristles short and irregular; posteroventral bristles much stronger, becoming as long as femoral diameter apically. Mid tibia with two anterodorsal and four posterodorsal bristles. Hind legs as in Fig. 9; femur with numerous strong short anteroventral and posteroventral bristles medially; hind tibia tapering evenly from base to middle and slightly compressed laterally, then suddenly compressed laterally just beyond the middle, and expanding into a swollen apex, the inner surface with a mat of close-packed setulae; hind metatarsus distinctly swollen.

Abdomen.—Brown in ground color; distinctly brown pollinose dorsally, grey pollinose ventrally; hairs black. Hypopygium as in Fig. 24; cercal plate large and broad, truncate apically, sparsely setulose; tergal plate directed dorsally, tapering strongly to middle, then slightly swollen with a rounded apex bearing numerous setulae, those on dorsal surface bristle-like; aedeagus long and whip-like.

Female

Head.—Frons grey-brown, bearing three or four pairs of small frontal bristles.

Thorax.—Wing medium brown.

Legs.—Color as in the male. Mid femur setulose except for a distinct row of posteroventral bristles on apical half. Mid tibia with three distinct anterodorsal, two distinct posterodorsal, and several weaker anteroventral and posteroventral bristles. Hind femur setulose, setulae slightly longer on anterodorsal and posteroventral surfaces, but not pennate. Hind tibia with irregular rows of short anterodorsal and posterodorsal bristles.

Abdomen.—Color as in the male.

Types

Holotype.— ♂, Aylmer, Quebec, 16.V.1924 (C. H. Curran) C.N.C. No. 6706.
Allotype.— ♀, Low Bush, Lake Abitibi, Ontario, 2.VI.1923 (N. K. Bigelow).
Paratype.— ♀, Laniel, Quebec, 17.VI.1933.

Rhamphomyia (Pararhamphomyia) valga Coquillett

Figs. 10, 21

Rhamphomyia valga Coquillett, 1895, p. 428; Melander, 1925, p. 209.

This species is quite distinct from all others of the group in that the hind legs are simple except for the elaborate knee-joint. Additional characters are the long style, and numerous dorsal bristles on the hind tibia. The females are easily recognized by the strongly pennate middle and hind legs. Length 3.5-3.8 mm.

Male

Head.—Antenna with basal segments yellowish; third segment two and a half times as long as broad; style almost half as long as third segment. Occipital bristles black, the row usually interrupted on side of head. Postoccipital bristles strong, black, in a single, usually regular row. Ventral bristles slender, black.

Thorax.—Pale brownish-grey pollinose, with distinct brown acrostichal and dorsocentral vittae, bristles black. Propleuron medially bare. One sublateral bristle, three supraalars, two intraalars, three weak humerals, and one or two anterior notopleurals. Squama pale yellow with light brown hair-fringe. Knob of haltere pale yellow. Wing faintly infuscated.

Legs.—Entirely infuscated, knees paler; bristles black. Fore coxa with seven or eight strong bristles. Mid femur with anteroventral bristles short, strong, regular; posteroventral bristles longer and somewhat irregular. Mid tibia with zero to two anterodorsal bristles. Hind leg as in Fig. 10; femur with anteroventral bristles weak on basal half, strong preapically, posteroventral bristles slender, long basally, decreasing evenly to setulae at apex; hind tibia with several distinct anteroventral bristles at base, and numeral long irregular anterodorsal bristles; hind metatarsus scarcely swollen.

Abdomen.—Brownish in ground color; venter pale; hairs dark brown. Hypopygium as in Fig. 21; cercus quite small and spatulate; tergal lobe directed dorsally, very broad at base, narrowing strongly to just before apex, with small apical portion rounded and with numerous bristle-like setulae.

Female

Head.—Frons pale grey, bearing two or three pairs of small frontal bristles.

Thorax.—Wing only weakly infuscated.

Legs.—Color as in the male. Mid femur and tibia with anterodorsal and posteroventral surfaces very strongly pennate, other surfaces setulose. Hind femur and tibia with anterodorsal and posteroventral surfaces long pennate, anteroventral and posterodorsal surfaces short pennate to setulose. Hind metatarsus dorsally short pennate.

Abdomen.—Color as in the male.

Type Locality and Type

New Hampshire. Holotype male in U.S. National Museum No. 3217, examined by me in April, 1958.

Material examined 31 ♂♂, 32 ♀♀.

QUEBEC. Indian House Lake, 25 ♂♂, 32 ♀♀, 20.VII.-16.VIII.1954 (W. R. Richards), 1 ♂, 6.VII.1954 (R. Coyles); Fort Chimo, 1 ♂, 9.VII.1954 (E. E. Sterns), 1 ♂, 7.VII.1954 (J. F. McAlpine); La Ferme, 1 ♂, 1.VII.1943 (A. Robert). LABRADOR. Goose Bay, 1 ♂, 2.VIII.1947 (W. E. Beckel). NEWFOUNDLAND. Fogo Island, 1 ♂, .VII.1929 (C. W. Johnson coll'n.).

Rhamphomyia (Pararhamphomyia) hypsela n. sp.

Figs. 12, 22

This species and *tolucensis* form a group quite distinct from other species of the group in having slender hind legs with the femorotibial joint only slightly

enlarged. The apically expanded male hind tibia and bristled female hind tibia separates this species from the following one. Length 3.5-3.8 mm.

Male

Head.—Antenna with basal joints dark reddish-brown; third segment three times as long as broad; style one-third as long as third segment. Occipital bristles black, distinct only on dorsal half. Postoccipital bristles black, numerous, irregularly situated. Ventral bristles long, black.

Thorax.—Dark greyish-brown with no brown pollinose vittae but with a pair of reflecting vittae between dorsocentral and acrostichal bristles visible from in front, bristles black. Propleuron medially bare. One or two sublateral bristles, two or three strong supraalars, a few weak intraalars, two to four weak humerals and four to eight anterior notopleurals. Squama medium brown with black hair-fringe. Knob of haltere greyish yellow. Wing faintly infuscated; veins brown.

Legs.—Black, not even knees yellowish. Fore coxa with three to five anterior bristles. Mid femur with anteroventral bristles decreasing evenly to apex; posteroventral bristles similar, slightly longer. Mid tibia with three anterodorsal and two or three posterodorsal bristles. Hind leg as in Fig. 12; femur with anteroventral bristles equal in length, in a regular row, posteroventral bristles similar; hind tibia enlarging rather evenly to apex; hind metatarsus not or scarcely swollen.

Abdomen.—Dark greyish-brown pollinose throughout; bristles black. Hypopygium as in Fig. 22; cercus wide at base, broadened on apical fourth; tergal lobe broad basad, with a broad concavity medially on ventral surface and a sudden narrowing preapically on dorsal surface, apex with several short bristles; subcercal process quite broad, with a broad preapical dorsal excision.

Female

Head.—Frons brownish-grey, with three to four pairs of frontal setulae.

Thorax.—Wing slightly darker than in the male.

Legs.—Color as in the male. Mid femur with anteroventral and posteroventral bristles short, strong, increasing evenly to apex. Mid tibia with two anterodorsal, one posterodorsal, and a full row of short strong posteroventral bristles. Hind femur with a full ventral row of short and only slightly pennate setulae, anteroventral bristles distinct only on apical half, posteroventral bristles setulose, anterodorsal setulae erect preapically but not flattened. Hind tibia with three distinct anterodorsal bristles.

Abdomen.—Subshining, weakly brownish-grey pollinose, hairs black.

Types

Holotype.—♂, West Side of Cortes Pass, 9500 ft., Mexico, Mexico, 13.VIII.1954 (J. G. Chillcott). C.N.C. No. 6707.

Allotype.—♀, same data, collected at 11,000 ft.

Paratypes.—2 ♂♂, same data as holotype.

Rhamphomyia (Pararhamphomyia) tolucensis n. sp.

Figs. 11, 23

This species is very close to *hypsela*, but differs in that the male hind femur is strongly bristled and medially constricted and the hind tibia is of even diameter throughout; while the female hind femur and tibia are distinctly pennate. In addition the propleuron is bristled medially. Length 3.6-4.1 mm.

Male

Head.—Antenna with basal joints black; third segment three times as long

as broad; style one-fourth as long as third segment. Bristles as described for *hypsela*.

Thorax.—Color as described for *hypsela*. Propleuron medially with two or three setulose bristles. Two or three sublateral bristles, two or three supraalars, several weak intraalars, seven or eight weak humerals, and about eight weak anterior notopleurals. Squama medium brown with black hair-fringe. Knob of haltere distinctly infuscated. Wing faintly infuscated; veins brown.

Legs.—Black, bristles black. Fore coxa with three to five anterior bristles. Fore femur with a distinct row of posteroventral bristles on apical half. Mid femur with anteroventral bristles short, alternately strong and weak; posteroventral bristles slightly longer, less regular. Mid tibia with three strong anterodorsal and two weak posterodorsal bristles. Hind leg as in Fig. 23; femur with strong ventral and anteroventral bristles on basal and apical thirds with short sparse bristles on median third; hind tibia subequal in diameter throughout; hind metatarsus not or scarcely swollen.

Abdomen.—Dark greyish-brown pollinose throughout; bristles black. Hypopygium as in Fig. 23; cercus directed dorsally, broad at base with a curved ventral surface; tergal lobe tapering more or less evenly to apex, slightly curved upwards near the tip, apex with several short bristles; subcercal process broad throughout, somewhat excised preapically on dorsal surface.

Female

Head.—Frons brownish-grey with three to five pairs of small frontal bristles.

Thorax.—Wing slightly darker than in the male.

Legs.—Color as in the male. Mid femur with anterodorsal bristle row becoming stronger apicad, very bristle-like on apical third; dorsal bristles weakly pennate. Mid tibia without distinct bristles, anteroventral and posteroventral setulae weakly pennate. Hind femur with anteroventral and posterodorsal surfaces strongly pennate, anterodorsal and posteroventral surfaces weakly pennate. Hind tibia with anteroventral and posterodorsal surfaces weakly pennate.

Abdomen.—As described for *hypsela*.

Types

Holotype.—♂, 10 miles east of Toluca, 8,900 ft., Mexico, Mexico, 31.VII.1954 (J. G. Chillcott). C.N.C. No. 6708.

Allotype.—♀, same data as holotype.

Summary

The *Rhamphomyia* (*Pararhamphomyia*) *basalis* group is distinguished from the other groups of *Rhamphomyia* by an enlarged femorotibial joint on the hind leg of the male and by broad wings and usually pennate legs in the female. Twelve species are included, of which eight are new. Except for two species from Mexico, all New-World species are restricted to northeastern North America. Immature stages are known to live in decaying wood. Keys are given for both males and females, detailed descriptions are given, and male hind legs and hypopygia are figured for all species.

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The Assessment of Larch Sawfly Cocoon Predation by Small Mammals[1]

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Introduction

Current investigations at the Forest Biology Laboratory, Winnipeg, are being directed towards the formulation of life tables for the larch sawfly, *Pristiphora erichsonii* (Htg.) (Lejeune, 1955). Because small mammal predation is a major factor in reducing cocoon populations of the sawfly (Buckner, 1953), an adequate method of assessing this source of mortality is desirable.

Five methods for estimating the amount of small mammal predation on larch sawfly cocoons were tested. A modification of the cocoon planting technique suggested by Graham (1928) provided the most useful means of assessing small mammal predation, from the standpoint of life table utilization. The usefulness of the other techniques for specific problems will be discussed.

Methods and Results

The Cocoon Planting Techniques

Cocoon planting for the assessment of small mammal predation on larch sawfly cocoons was first used by Graham (1928), and later tested by Morris (1949) for the European spruce sawfly. These authors planted at regular intervals throughout the plot, 100 sets of five (later three) cocoons enclosed in small cotton bags. Periodic examination of these plantings showed the percentage of predation by small mammals. These authors found that the mammals chewed both cotton bags and cocoons beyond recognition, and so considered each set as a unit. The present author modified the technique so that each cocoon could be considered as a unit, and could be reclaimed for subsequent examination. This was accomplished by wiring apparently sound cocoons to three-inch tree tags. Two cocoons were placed about two inches apart on each tag. The cocoons were buried in tamarack bogs to a depth of approximately two inches, leaving about one inch of the tag projecting above the ground. One hundred sets were planted at intervals of about 40 feet in each bog. These were examined at intervals and the condition of each cocoon recorded. The technique is of advantage because each cocoon, rather than each set, can be recorded as a unit, and the order of the predator can be determined by the markings left on opened cocoons (Buckner, 1958).

During the period from 1952 to 1954, each cocoon opened by a small mammal was replaced as the sets were examined. Using the replacement modification,

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TABLE I

Comparison of cocoons on tags and loose cocoons opened by small mammals in cages

Predator	Cocoon type	Total	% Opened	Chi-square	d.f.	P.
Sorex cinereus (20)	Loose	1560	91			
	On tags	800	94	.531	1	.5 approx.
S. arcticus (20)	Loose	1560	97			
	On tags	800	89	16.3	1	less than .01*
Clethrionomys gapperi (10)	Loose	780	73			
	On tags	400	68	802	1	.4 approx.
Microtus pennsylvanicus (2)	Loose	78	72			
	On tags	40	78	.444	1	.5 approx.

*Difference significant at less than one per cent level.
Bracketed numbers indicate number of animals tested.

sets of cocoon plantings were examined at weekly intervals, at monthly intervals, and only once during the season, after small mammal predation had ceased. The various methods yielded essentially the same estimate of predation. On one plot during the late summer and fall of 1953 and the spring of 1954, the accumulated predation was 77 per cent when the sets were examined at weekly intervals, 72 per cent when examined at monthly intervals, and 79 per cent when examined only after predation had ceased. If the sets are examined at weekly intervals and the cocoons replaced as they are opened, a larger weekly sample is available. However, the replacement technique was abandoned in 1955 in order to gain additional information as explained later in this paper.

There is a possibility that cocoons on tags influence the feeding behaviour of small mammals by acting either as an attractant or repellent. To test this possibility, a cage with about 36 square feet of floor space was filled with sphagnum moss to a depth of about five inches, and cocoons on tags as well as loose cocoons were buried in the moss. Various small mammal predators were introduced and the numbers of opened tagged and loose cocoons were compared using pooled 2 x 2 Chi-square tests. The results are given in Table I. These data suggest that *Sorex cinereus cinereus* Kerr., the cinereous or masked shrew, *Clethrionomys gapperi loringi* (Bailey), the red backed vole, and *Microtus pennsylvanicus drummondii* (Audubon and Bachman), the meadow vole, are not influenced by the tags. The tags may repel *S. arcticus laricorum* Jackson, the saddle-backed shrew, to some extent.

Four replicates of the cocoon planting technique gave statistically consistent results.

Other uses for the cocoon planting technique include the determination of favourable and unfavourable locations for predation, and the effect of cocoon depth on predation (Buckner, 1958).

The Collection Rate Technique

The collection rate technique consists of collecting cocoons in an area at specified intervals of time before and after the period of small mammal predation. The numbers of sound cocoons collected per units of time in each sample are compared, and the differences between pre- and post-predation samples are attributed to small mammal predation. In this experiment 12 sampling points were established at 20-pace intervals, and cocoons were collected for five minutes at each station. Adjacent samples were taken after small mammal predation had

TABLE II

Small mammal predation on larch sawfly cocoons assessed by the collection rate technique and the cocoon planting technique

Date	Location	Cocoons collected per hour		% predation	% predation (Planting technique)
		Before predation	After predation		
1952	Telford	231	122	47	63
	Red Rock Lake	287	158	45	48
1953	Telford	183	37	79	94
	Red Rock Lake	329	53	84	98

ceased and the number of cocoons collected per man-hour was then compared with pre-predation collections. The results are recorded in Table II and are compared with estimates based upon the cocoon planting technique.

The collection rate technique is not considered to be an accurate means for determining the relative abundance of cocoons since the mood of the investigator, the meteorological conditions, and the type of terrain may tend to influence the efficiency of the collector. The technique may be adequate where only trends are considered and is less time consuming than other procedures for rating predation.

The Cocoon Sampling Technique

The cocoon sampling technique is a modification of the collection rate technique. Predetermined stations are sampled before and after predation and the numbers of sound cocoons compared. The difference is attributed to small mammal predation. In this experiment 20 sampling stations were chosen at the bases of large trees and a one-square-foot sample was taken in a direction chosen at random before and after predation. The results are recorded in Table III, and compared with estimates based on the cocoon planting technique.

This technique shows reasonable agreement with the cocoon planting technique and is not susceptible to the errors of judgment and mood of the collection rate technique. However, where predation is high and the insect population low, very large samples in the post-predation stage would be required to assess predation with confidence.

The locations of sampling points in this experiment were chosen to give the maximum number of cocoons. If the technique were to be used to assess cocoon populations as well, a random distribution of sampling effort would be required.

TABLE III

Comparison of predation of larch sawfly cocoons by small mammals derived from estimates using the cocoon sampling and cocoon planting techniques

Plot	Pre-predation cocoon sample	Post-predation cocoon sample	% predation by cocoon sampling technique	% predation by cocoon planting technique
1	37	13	65	54
2	25	6	76	76
3	134	12	91	92
4	55	10	82	87
5	10	4	60	43

The Saturation Trapping Technique

The saturation trapping technique involves removing the entire small mammal population from an area by means of snap-back traps and comparing the emergence of adult sawflies on the mammal-free area with that on an area containing a normal complement of small mammals. A large, uniform tamarack bog was chosen for this experiment and two five-acre plots five chains apart were established. On one, the mammal population was removed by constant snap-back trapping, which began before mature larvae were falling from the trees and lasted until late October. The other plot retained its small mammal population and served as a control.

In the spring, 30 emergence cages were set out on each plot to sample the populations of surviving adults. Each of these cages covered an area of two square feet. The mammal-free plot yielded 222 adults, while on the undisturbed plot 102 were captured, indicating about 46 per cent predation on the plot containing mammals. Predation, as estimated by the cocoon planting technique, was 49 per cent. Although agreement between the two techniques was satisfactory, the results should be treated as indicative rather than conclusive, because the emergence cages in some instances allowed a proportion of the adults to escape.

Although the saturation trapping technique appears to provide a reliable estimate of small mammal predation on larch sawfly cocoons, it is not recommended for use in life tables. It is laborious and time consuming and requires a large uniform area that is usually unavailable in tamarack stands. Furthermore, the danger of permanently destroying the natural small mammal complement is high (Buckner, 1957), and this is not desirable in prolonged studies.

The Mammal Exclusion Cage Technique

The mammal exclusion cage technique consists of exposing known numbers of larch sawfly cocoons to small mammal predation while a control is excluded from predation by mammal-proof cages. An experiment of this nature was tested in the 1955-1956 field season. Cylindrical fine-wire screen cages with open bottoms and cotton drawstring tops were buried in the moss deep enough so that the bottom of the cage lay below the water table. Ten cages were set out on each of three plots. Thirty-five larvae in post-feeding stages were set on top of the moss in the cages and allowed to spin. Eight cages on each plot were removed soon after cocoon formation by opening the drawstring, placing one hand inside to hold the moss in place, and sliding the cage upwards and free from the moss. The remaining cages were used to estimate the number of larvae that actually formed cocoons. After small mammal predation had ceased, the moss from the caged and uncaged areas was examined and the number of sound cocoons recorded. Predation was then estimated by determining the percentage of cocoons formed in the exclusion cages, and, considering this as the number available to small mammals in the exposed areas, calculating the number missing and presumably destroyed by small mammals. A comparison between the exclusion cage and cocoon planting technique for the same period is given in Table IV.

The exclusion cage technique is similar to that of the saturation trapping technique. However it is less laborious, and the exclusion cages are simpler and more easily constructed than the emergence cages.

The exclusion cage technique appears to give a reliable estimate of small mammal predation on larch sawfly cocoons. It is adaptable to life table studies but has an inherent anomaly that has not been assessed. Whereas the cocoon planting technique adds 200 cocoons to an area of about five acres, the exclusion

TABLE IV

Comparison of the results of the exclusion cage and cocoon planting technique in determining small mammal predation on larch sawfly cocoons

Plot	% larvae that formed cocoons in exclusion cage	% predation on exposed areas	% predation from planting technique
1	87	51	54
2	91	80	76
3	87	95	92

cage adds a concentration of cocoons to a very localized area. Especially at low prey populations, these "pockets" of cocoons could conceivably act as a bait for small mammals and hence lead to an overestimate of predation.

Discussion

In the development of life tables for a forest insect, it is important to assess the mortality occurring in each age class or stage (Morris and Miller, 1954). Because small mammals have been shown to be important predators of larch sawfly cocoons, it is necessary to assess this source of mortality. Five techniques to assess small mammal predation on larch sawfly cocoons have been outlined in this paper, namely the cocoon planting, collection rate, cocoon sampling, saturation trapping, and exclusion cage techniques. Although it was not possible to test and replicate all five techniques simultaneously, series of comparable data were obtained for the cocoon planting and the remaining techniques individually. The results from each technique were compared with those from the cocoon planting technique and tested for significance using individual and pooled 2 x 2 Chi-square tests. These are recorded in Table V. The results indicate that there is no agreement on the assessment of predation between the cocoon planting and collection rate techniques. It will be noted that in every case, the estimate of small mammal predation based upon the collection rate technique was lower than that of the cocoon planting technique, although one trial is not significantly different. Possibly this indicates an unconscious effort on the part of the investigator to search more diligently in the post-predation collection. This is further emphasized, since the results of the cocoon sampling and cocoon planting techniques agree in three of the five trials, and disagreement is significant only where the sample sizes are very small. Since the cocoon sampling trials represent the examination of 200 cubic feet of moss, time and labour limited further testing of the technique. Where sufficient cocoons were recovered to make reliable comparisons with the cocoon planting technique, agreement was highly significant. Similarly, the results from both the exclusion cage and saturation trapping techniques agree favourably with those from the cocoon planting technique. Ives (1959) also finds agreement between predation as assessed by the planting technique and by a cocoon sampling technique. From these data it may be concluded that:

1. The cocoon planting technique is a reliable means for assessing small mammal predation on larch sawfly cocoons.

2. The collection rate technique is not a reliable means of assessing this source of mortality.

3. The cocoon sampling technique is probably a reliable method of estimating small mammal predation on larch sawfly cocoons, but often low populations of the prey insect and labour shortages preclude the use of the method.

TABLE V

Evaluation of the cocoon planting technique for estimating small mammal predation on larch sawfly cocoons by comparing with other techniques, using iudividual and pooled 2 x 2 chi-square tests

Technique		Trials										
		1	2	3	4	5	6	7	8	9	10	Total
Cocoon planting	Per cent	63	48	94	98	54	76	92	87	43	49	
	Sample	200	200	200	200	200	200	200	200	200	200	
Collection rate	Per cent	47	45	79	84							
	Sample	231	287	183	239							1030
	X^2	12.10**	.40	15.05**	24.8**							322**
Cocoon sampling	Per cent					65	76	91	82	60		
	Sample					37	25	134	55	10		261
	X^2					4.32*	2.78	.007	.99	4.49*		1.0
Exclusion cage	Per cent					51	80	95				
	Sample					242	254	243				739
	X^2					1.20	1.17	2.0				1.06
Saturation trapping	Per cent										45	
	Sample										222	
	X^2										1.6	

*difference significant at 5% level.
**difference significant at 1% level.

4. The exclusion cage and saturation trapping techniques give reliable estimates of small mammal predation on larch sawfly cocoons.

The cocoon planting technique has been used almost exclusively to provide an estimate of small mammal predation for life tables of the larch sawfly. Earlier estimates were made by examining the sets at weekly intervals and replacing chewed cocoons at each examination. However, it was found that small mammals differentiate to varying degrees between sound and parasitized cocoons, and to measure this interacting factor, all subsequent trials were examined at weekly intervals but without cocoon replacement. The sets were left in the ground until the adult sawflies had ceased emerging the following summer and the cocoons were then examined and recorded as being opened by mice or shrews, having sawfly emergence holes, emergence holes of parasites, attacked by fungus, dead, or apparently sound. By comparing the numbers from which sawfly had emerged, the apparently sound cocoons and the number with parasite emergence holes with determinations of parasitism made at the time of larval drop, the interacting effect of small mammal selection is estimated.

A 1954-55 "pilot" life table study provides an interesting example of the usefulness of the technique. The initial cocoon plantings were set out on August 11. At this time a large proportion of the larval population was still feeding. Cocoon populations were estimated by trapping mature larvae as they fell from the trees and allowing them to spin cocoons in special receptacles. This estimate was checked by random cocoon sampling during the first week of September. The estimated cocoon population per tree using the larval drop technique was 1,263 cocoons, and 218 by the cocoon sampling technique (Turnock, 1956). However, by correcting the latter estimate for the 37 per cent small mammal predation which had occurred to the time of cocoon sampling, and by adding to this other mortality factors to the time of sampling, the initial cocoon

TABLE VI
Partial life table for the 1954–55 generation of the larch sawfly in the Telford bog, Whiteshell Forest Reserve
(Abstracted from Turnock, 1956)

X Age interval	1x* No. alive at beginning of X	dxF Factor responsible for dx	dx No. dying during X	100 qx $\frac{dx}{1x} \times 100$
Cocoon (fall)	1263.2 (1030**)	parasites	128.2	10.1
		miscellaneous	533.8	42.3
		small mammal predators	475.0**	37.6**
		Total	1137.0	90.0
Cocoon (winter and spring)	126.2	unknown plus holdover	32.8**	26.0**
		parasites	34.0**	27.0**
		Total	66.8**	53.0**
Adult	59.4**	males	0.25	0.4

*Number per tree.
**Estimates provided by the cocoon planting technique.

population was estimated as 1,030 per tree (Turnock, 1956). Thus, the cocoon planting technique aided greatly in dispelling the discrepancy between two independant estimates of the cocoon population. By the last week in October predation had ceased, and 79 per cent of the planted cocoons had been destroyed by small mammals; 43 per cent by shrews and 36 per cent by mice. Mechanical difficulties prevented the use of emergence cages to assess the surviving adult population. By allowing the cocoon plantings to remain in position until after the adult emergence period it was estimated that of the cocoons that escaped small mammal predation, 47 per cent produced adults in the spring of 1955, and the tachinid parasite, *Bessa harveyi* (Tnsd.) emerged from another 27 per cent. Thus the cocoon planting technique provided information in addition to mammalian predation. Table VI is a partial life table showing estimates provided by the cocoon planting technique.

The use of the cocoon planting technique exclusively for determining small mammal predation of larch sawfly cocoons may not be desirable, because total reliance on one technique without adequate checks may introduce errors. For example, it has been shown (Buckner, 1958) that under certain limited circumstances small mammal predation varies with cocoon depth. If the cocoon population were concentrated very close to the water table, small mammal activity would be inhibited and the cocoon planting technique would tend to give an overestimate of the percentage of cocoons destroyed by small mammals. Or, if the cocoon population were concentrated deeply, a rising water table could submerge and kill them. The predation on this population as estimated by the cocoon planting technique would give a good approximation for the remaining cocoons, but a false impression of the main mortality source. In order to avoid such errors, the cocoon planting technique should be supplemented.

The choice of a secondary technique could be made after a decision on the technique for estimating cocoon populations in the life table project has been reached. Current techniques used in the life table project include both larval drop and random cocoon samples. Random cocoon samples taken after predation

has ceased can be readily compared with cocoon samples taken during life table studies and thus provide a check against the planting technique.

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Joint Annual Meeting of Entomological Society of Canada Entomological Society of Ontario, and Entomological Society of America, Detroit, November 30 to December 3, 1959

The Entomological Society of Canada, the Entomological Society of Ontario, and the Entomological Society of America will hold their annual meetings jointly at Detroit, Mich., Nov. 30 to Dec. 3, 1959.

The June issue of the Bulletin of the Entomological Society of America will present the highlights of the program and the call for papers; the October issue will contain the complete program. By arrangement between the societies, these issues will be distributed to all members of the Entomological Society of Canada.

Canadians have always been generously represented in the membership and offices of the Entomological Society of America. The combined meeting of the societies will be a fruitful continuation of this tradition of common interest.

B & Z Library

A Study of the Flight of the Douglas-Fir Beetle, *Dendroctonus pseudotsugae* Hopk. (Coleoptera: Scolytidae) I. Flight Preparation and Response[1]

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Insect flight can be divided into four basic components which lend themselves to independent study. These are: (1) flight preparation and response; (2) the body movements and their resultant forces; (3) the flight capacity; and (4) flight orientation. Many authors have dealt with these various phases of flight and studies have been made on a wide variety of insects. Nevertheless, on reviewing the literature two deficiencies become apparent. First, there are very few cases where a complete study of flight has been made for a single species, an outstanding exception being the studies on locust flight by Weis-Fogh and Jensen (1956). Secondly, beetles, particularly the Scolytidae, have been neglected as experimental material in flight studies.

The Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopk., has given considerable concern to members of the logging industry in the interior of British Columbia, necessitating an understanding of its biology and behaviour. Although this insect flies for only a few brief periods during its life, it is a phase of behaviour that is vital to its success and important in the extension and location of areas of infestation.

In this paper I shall deal with the initial phase of flight, the preparation and response, in an attempt to add to our fundamental knowledge of bark beetle behaviour.

The studies were conducted in the vicinity of Vernon, Lac la Hache, and Victoria, B.C., from 1956 to 1958.

Flight Preparation

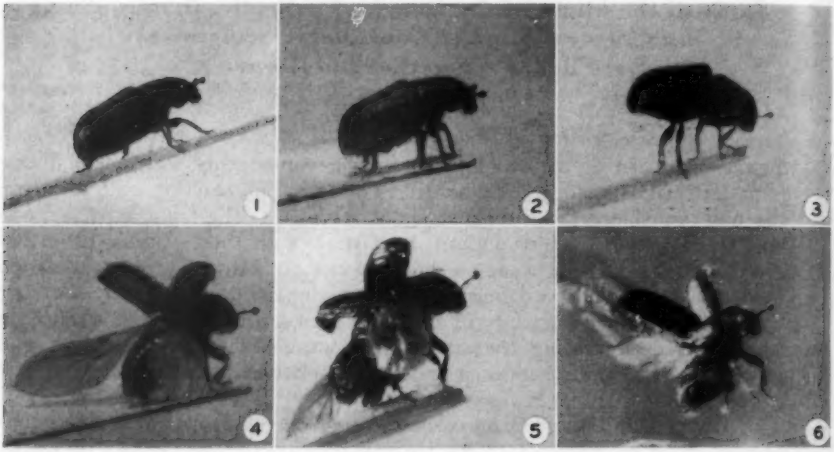
Before flying, many insects pass through a series of preflight movements; the Douglas-fir beetle is no exception. In the still air of the laboratory at 23° C., the beetles usually walked towards the light. Under conditions of nearly even lighting they wandered seemingly at random over a flat surface, although many individuals walked up an inclined surface. In gently moving air most of the beetles walked into the flow. The amount of walking varied widely from a few seconds to long periods without a flight attempt.

Just prior to taking flight, the beetles stopped walking (Fig. 1) and slowly waved their antennae. The legs were then raised and lowered in turn, as if to plant the tarsi firmly on the substrate, after which the pro- and mesothoracic legs were arched and the hind legs were bent towards the rear, tilting the body backwards (Fig. 2). This position was maintained for varying lengths of time during which there was noticeable pumping of the abdomen. Eventually, either the body was quickly rocked forward and the elytra partially opened (Fig. 3) or walking was resumed. The loosening of the elytra over the wings was immediately followed by a backward tilt of approximately 45 degrees ending with the wings fully extended (Fig. 4). Another brief pause occurred in this position during which the mesothoracic legs were lifted to their flight position below the posterior margin of the elytra (Fig. 5). This was followed by a straightening of the hind legs producing a jump which initiated flight (Fig. 6).

Flight Response

The response phase of insect flight is important because it is the initial func-

[1]Contribution No. 524, Forest Biology Division, Science Service, Department of Agriculture. Ottawa, Canada. Based on studies for a thesis to be submitted to the Faculty of Graduate Studies of the University of British Columbia in partial fulfilment of the requirements for a Master of Arts Degree.



Figs. 1-6. The pre-flight movements and take-off of the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopk.

tion that changes the insect's position in its environment and brings an entirely new complement of forces into action. Since an individual will not respond positively under unsuitable conditions, a study of the stimuli involved in the promotion of flight should reveal the optimum conditions for the activity while at the same time exposing any stimuli which may enable the insect to fly under sub- or extra-optimal conditions. This is particularly important in insects such as the Douglas-fir beetle, as the basic factor of temperature may be suboptimal while the humidity might be extra-optimal during the spring flight period.

The Effect of Associates on the Flight Response

Two hundred young adults which emerged in May and July from overwintered logs were collected daily in samples of 20 or 30 and placed in petri dishes containing moist paper. When the room temperature reached 22° to 23° C., each individual was stimulated to fly by tossing. As for many other insects (Roeder, 1953), tossing produces a strong flight stimulus for the Douglas-fir beetle. After three tosses each beetle was classified as to response according to the following categories.

1. *Good* – The flight was strong following a rapid response.
2. *Poor* – The response was slower and the flight was weak.
3. *Flutter* – The beetle dropped with wings vibrating insufficiently for organized flight.
4. *Negative* – Either there was no visible positive response or the wings were extended but not vibrated.

Following the determination of the response of each beetle, dissections were made to determine the sex, gut condition (material present or absent), and the presence or absence of mites and nematodes.

Since the number of possible combinations in these data is great and the range of the degree of associate infestation was wide the results do not lend themselves to simple analysis. Therefore the data are condensed in Table I, omitting sex and gut condition, which obviously had no effect. From these results it appears that the presence of mites and nematodes had little or no effect on the insects' flight response, at least when a strong stimulus was applied.

TABLE I
Flight response following stimulation and results of dissection of 200 Douglas-fir beetles

Response	Total	Associates absent	Nematodes			Mites only	Mites and nematodes
			Internal only	External only	Internal & external		
Good	150	26	8	32	6	17	61
Poor	13	0	1	3	0	1	8
Flutter	15	2	2	1	1	2	7
Negative	22	4	0	6	2	2	8
Total	200	32	11	42	9	22	84

In order to establish whether or not these associates affected the normal flight reflex, 50 beetles were placed on a flat surface at 23° C. and 50 foot-candles in still air and allowed to move at will. As the beetles flew, they were captured and noted as having a positive response. Those which did not fly within a period of 15 minutes were considered negative. Dissections were made to observe the previously mentioned features. The results summarized in Table II show that the associates did not have any effect on spontaneous flight.

To date, identifications indicate that there are at least 18 species of nematodes, belonging to 10 genera, associated with the Douglas-fir beetle. This, as well as the complexity of nematode life histories, the lack of knowledge on their host relations and the difficulty with which they are identified, makes it impossible to determine if any one species had an effect. Even if the adults could be identified easily it would not necessarily mean that accompanying larvae were of the same species.

Most of the nematodes occurring internally were *Aphelenchulus* spp., *Aphelenchoides* sp., and *Sphaerularia* spp., which are believed to be true parasites (Van Zwaluwenberg, 1928; Massey, 1956). The most commonly occurring nematodes under the elytra were rhabditoids and *Diplogaster stercorarius* Bovien, believed to be commensals or mechanical associates (Van Zwaluwenberg, 1928) and *Aphelenchoides* sp. The *Aphelenchoides* found externally were invariably in the larval stage and may have been mechanical associates. Fuchs (1930) stated that larval *Diplogaster* spp., and rhabditoids carried under the elytra of bark boring beetles were in a resting stage and thus named them "Dauerlarven".

TABLE II
Spontaneous flight response and results of dissection of 50 Douglas-fir beetles

Response	Total	Associates absent	Nematodes			Mites only	Mites and nematodes
			Internal only	External only	Internal & external		
Positive	41	16	18	4	3	0	0
Negative	9	4	2	2	1	0	0
Total	50	20	20	6	4	0	0

On the basis of these facts, one would expect the internal species to represent the most serious drain on the beetles' reserves and have the greatest effect on their behaviour. Since these studies have shown that the nematodes did not affect the flight response, it might be reasoned that the beetles are agents of nematode dissemination and are thus unaffected by their presence at this stage, although Massey (1956) and Reid (1958) suggest that they affect the beetles during other activities.

The mites which occurred externally were mostly nymphs of the genera *Digamasellus* or *Dendrolaelaps* and adults of *Vidia* sp., and *Uropoda* sp. found under the elytra, where there is evidence that they feed on the nematodes occurring in that region. The internal mites identified were all hypopi of *Vidia* sp.

The genus *Digamasellus* is usually found associated with bark beetles and may be predacious or mycetophagous. *Vidia* are usually found associated with wasps although they comprise a group about which very little is known. *Uropoda* are of no economic or medical importance but frequently attach themselves to insects for dissemination and probably do not harm their hosts (Morgan, in litt.).

The Effect of Temperature on the Flight Response

Four samples of 25 young adults each were placed in open but shaded petri dishes of moist paper at the prevailing temperature and allowed to walk at will and make voluntary flight attempts. Ten minutes later each beetle was tossed three times and classified according to response. Upon completion of the test the beetles were placed in closed petri dishes until the temperature increased a few degrees, at which time they were retested. This test was conducted at six or seven different temperatures with each sample of beetles.

At 14° to 15° C., the beetles walked around the dishes and in a few cases extended their wings. At 18° to 19° C., several unsuccessful flight attempts were observed while at 20° C., three of 50 beetles made successful flights to a window a few feet away. If the petri dishes were moved into direct sunlight many beetles made successful flight attempts at air temperatures from 17° to 20° C. From 22° to 32° C., almost all the beetles made successful voluntary flights in the shade. At temperatures ranging from 32° to 36° C., only a few flights occurred; the majority of the beetles crawled around the edges of the dishes or under the paper, demonstrating a change in phototaxis. These findings vary only slightly from those of Rudinsky and Vite (1956).

On the other hand, when the same beetles were tossed throughout the range of temperature used (14° to 36° C.) there was little variation in the response. At 14° to 15° C. only 20 per cent of the beetles were flight negative and at temperatures above 30° C., only 16 per cent showed a negative response. In addition, at temperatures from 18° to 30° C., five to 10 per cent of the beetles consistently were flight negative.

The effect of temperature on flight response might be an important factor during the spring flight period owing to the lower temperatures which occur at that time of year. If the air temperature was below 68° F., as it often is during May in the interior of British Columbia, the beetles would require some additional flight stimulus. This would have to be in the form of sunlight since the chances of large numbers of beetles being stimulated by loss of tarsal contact are small. If the cool conditions were accompanied by cloudy weather, the periods suitable for the initiation of flight would be limited. During such years the population might be forced to limit its activity to the immediate vicinity of the previous in-

TABLE III
Results of increased flight stimulation on 100 Douglas-fir beetles

Toss	Response		No. changed to a positive reponse
	Negative	Positive	
1	39	61	
2	22	78	17
3	16	84	6
4	12	88	4
5	11	89	1
6	10	90	1
7	10	90	*

*No additional changes up to and including the tenth toss.

festation, whereas in a year with a warm and/or clear spring the population might disseminate more widely and start new centres of infestation.

The Effect of Increased Stimulation on the Flight Response

A sample of 100 young adult beetles was taken during the May emergence and stored overnight in petri dishes of moist paper. The following day, at 23° C., each beetle was tossed ten times and the response resulting from each toss was recorded. The results of this test, presented in Table III, show that the number of beetles which responded positively increased with stimulation up to and including the sixth toss.

The Effect of Gallery Extension on the Flight Response

A number of Douglas-fir beetle galleries were tagged on the day of initiation and opened at various stages of development from one to 40 days later. When a gallery was examined the parents were numbered for transport to the laboratory, and the length of the gallery and the number of eggs deposited therein were recorded. In the laboratory the parent beetles were sexed according to the methods described by Chapman (1955) and then tossed three times. The flight response was recorded as either positive, opened elytra, or negative.

In the summary of the results shown in Table IV, the numbers of beetles which responded by opening their elytra have been omitted since this response cannot satisfactorily be classed as either positive or negative.

It is evident that some females would fly during the first 24 hours of gallery construction, but once egg laying had begun, or was about to begin, all the females tested showed a negative response for the following 14 days. The remaining flight positive females were taken from galleries 15 to 25 days old. On the other hand, some males in the samples taken during the first ten days of gallery extension were flight-positive, as were some throughout the reoccurrence of flight-positive females. In addition, the sex ratio of adult beetles in the galleries examined changed in favour of females from close to 1:1 during the first week of excavation to 3:2 after 10 days and 2:1 after 13 days. Also, a sample of beetles which had emerged from a log attacked 10 to 14 days previously contained mostly males, all of which were flight positive. It seems that, unlike the females, some males are capable of flight throughout the first three weeks of

TABLE IV
Summary of the effect of gallery age from 1 to 40 days on the flight response of the Douglas-fir beetle

Gallery age in days	No. of galleries examined	Average length of galleries in inches	Average No. of eggs per gallery	Response in per cent of total of each sex[1]			
				Positive		Negative	
				F	M	F	M
1	25	Through outer bark	none	14.3	36.8	38.1	15.8
2–3	15	.50	.4	0.0	44.4	80.0	22.3
4	10	.85	.8	0.0	60.0	70.0	0.0
5	10	1.12	2.3	0.0	40.0	50.0	20.0
7	24	1.47	6.5	0.0	17.6	56.5	41.2
10	12	2.18	8.5	0.0	12.5	91.7	50.0
12	12	2.70	10.0	0.0	0.0	100.0	62.5
13	9	2.77	9.6	0.0	0.0	100.0	0.0
15	12	4.15	13.5	8.3	16.6	41.5	33.6
18	20	6.21	19.7	15.0	20.0	55.0	40.0
21	13	7.13	31.0	7.2	14.3	78.5	28.6
25	15	7.83	47.7	6.7	20.0	86.6	20.0
28	13	4.2[2]	25.6	0.0	0.0	71.4	33.3
31	9	4.9[2]	25.7	0.0	0.0	100.0	100.0
34	10	5.6[2]	37.7	0.0	0.0	100.0	60.0
40	15	5.5[2]	39.0	0.0	0.0	91.7	25.0

[1]Values for opened elytra response equal residual of 100 per cent.
[2]Galleries taken from a different source.

gallery construction and that if all the males originally involved in the galleries examined had been present in the samples taken, the positive response of males would have been more common. The lack of positive response by either sex after 25 days may indicate that any beetles which leave their galleries following the first four weeks are unable to fly.

These observations indicate that something took place rapidly within the females changing their response within one day of the initiation of their galleries. Since this coincided with the beginning of oviposition it may, at first, have been due to the maturation of the ovaries and their intrusion into the pterothorax. The fact that some females reacted positively to flight stimulation from 15 to 25 days after attack is of interest, since it coincided with the time that most of the second attacks occurred in cage studies. Examination of the indirect flight muscles made in preliminary studies on their degeneration (Atkins and Farris, 1958) showed that changes occurred in the flight muscles of females soon after the galleries were initiated and that there was no sign of regeneration even after 50 days as was found in the mountain pine beetle, *Dendroctonus monticolae* Hopk., (Reid, 1958). Nevertheless, there were always a few females taken at each gallery age which did not show flight muscle degeneration. These apparently normal females would appear to be the only ones capable of a second flight two to three weeks after the first attack. Furthermore, since the muscles of these females do not change, it is possible that they are predestined to make a second attack. Some would be prevented from showing a positive flight response during the first two weeks of gallery extension by the production and deposition of eggs. Those which could fly during this period probably left their galleries and thus were not included in the samples taken.

McMullen and Atkins (unpublished data) have shown that after 30 days the percentage of parents which abandoned their galleries increased with attack density and that less eggs were laid per inch of gallery at higher attack densities. It seems either that the greater number of females which left their galleries at higher densities may be related to the deposition of fewer eggs, or that some of the females that left were not capable of flight and were lost.

The Effect of Light Intensity on the Flight Response

A number of newly emerged adults that showed a strong positive response to 10 foot-candles (one foot-candle = 10.764 lux). As individuals made voluntary flights they were removed from the test area and placed in numbered vials. The beetles which had not flown after 10 minutes (25 per cent) were considered negative. The test was repeated at 0.5, 2, 15, 35, 65, 300 and 500 foot-candles within a temperature range of 23° to 25° C.

No beetles flew at 0.5 foot-candles. At two foot-candles the reaction was slow and during the ten-minute trial only 45 per cent of the beetles flew. At 15 and 35 foot-candles, 25 per cent failed to fly, while at the remaining light intensities all but one beetle (the same individual in each case) flew. However, the speed of reaction appeared to increase with the light intensity.

In order to establish whether or not the light intensity had any effect on the speed with which the beetles made spontaneous flights an additional test was conducted. Each of five samples of 20 flight positive beetles were released at five light intensities (2, 15, 35, 65 and 250 foot-candles) within the same temperature range as above, with a short rest period in darkness between trials. The time required for each beetle to take flight was recorded. The average reaction time of the first 10 beetles in each case was considered to be the value for the corresponding light intensity. The tests were conducted with both increasing

TABLE V
The speed of flight reaction of the Douglas-fir beetle in relation to light intensity

Light intensity in foot-candles	Average reaction time in seconds[1]	Percentage of sample that reacted
0.5	no reaction	—
2.0	284	45
15.0	142	75
35.0	122	95
65.0	117	95
250.0	53	95

[1]Value obtained from the first 50 per cent of sample to react.

and decreasing light intensity in order to reduce the error that may arise from adaptation or fatigue. The results are presented in Table V.

From this study it can be assumed that the Douglas-fir beetle does not fly during the nocturnal hours, although some are capable of flight under almost all daytime light intensities. However, since the speed of reaction is dependent upon the light intensity, light may be an important factor during the spring when low intensities might be inter-related with other factors falling near the threshold for flight.

Summary

Flight preparation and the effect of several factors on the flight response of the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopk, were studied. Infestation by mites and nematodes did not affect the beetles' natural flight response nor their response when a flight stimulus was applied.

Temperature had a marked control over the flight response although it could be overcome, within limits, by applying an extra stimulus. The optimum temperature for spontaneous flight was found to be between 22° and 32° C.

Individual differences between beetles were demonstrated by the effect of increased stimulation on the flight response. , About 50 per cent more beetles flew following five tosses than following the first toss.

Once gallery construction had begun the female beetles lost their ability or inclination to fly, but some showed a later positive response to flight stimulation after 15 days in their tunnels. The males did not entirely lose their positive response until the galleries were one week old but were again ready to fly along with the females.

The Douglas-fir beetle took flight at light intensities ranging from two to 500 foot-candles, but the speed with which they reacted increased as the light intensity increased.

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Book Review

The Odonata of Canada and Alaska, Volume Two, by Edmund M. Walker, Professor Emeritus of Zoology, University of Toronto, Honorary Curator of Zoology, Royal Ontario Museum of Zoology and Palaeontology. xi + 318 pp. 64 pls. University of Toronto Press, December, 1958. Price $13.00.

Five years ago (Canad. Ent. 86: 500, 1954) I had the pleasure of drawing the attention of readers to Volume One of this important work. It was then envisaged that a second volume, when published, would include a complete account of the remainder of the Odonata, viz., the suborder Anisoptera. Volume Two has now appeared, but for several reasons, as explained in a "Foreword" by Dr. F. A. Urquhart, it has seemed preferable to restrict it to a consideration of four families (the Aeshnidae, Petaluridae, Gomphidae, and Cordulegastridae) of the Anisoptera, and to leave the remaining three families (the Macromiidae, Corduliidae, and Libellulidae) to be dealt with in a subsequent and final volume.

Volume Two begins with an account of the general characteristics of the Anisoptera and a key to the aforementioned seven families of this suborder. This is followed by a detailed acount of the species in the first four families. Sixty-four species are included. These are contained in 15 genera, disposed as follows: Aeshnidae (seven genera, 23 species), Petaluridae (one genus, one species), Gomphidae (six genera, 36 species) and Cordulegastridae (one genus, four species). This compares with the total of 150 species, in 24 genera, included in the same families in the recent "Manual of the Dragonflies of North America", by

Needham and Westfall. As in Volume One, there are keys to the adults and nymphs for the recognition of the higher groups and the species, and elsewhere both are more fully characterized. Likewise, the accounts of the species are usually supplemented by the author's original illustrations, and are replete with a variety of information on habitats, behaviour, distribution and abundance.

In two features the present volume differs somewhat from Volume One. A more strictly morphological terminology in describing odonate structures, especially those of the nymphs, has been adopted as a result of the agreements and findings of recent workers (notably the work of Snodgrass, in 1954, on the larval dragonfly). Secondly the Tillyard-Fraser system of wing venation is introduced, because, as the author states, "we believe it rests on a sound foundation. In any case it is too important a contribution to be ignored". The text (pp. 5-9) therefore contains a detailed discussion of the Comstock-Needham and the Tillyard-Fraser systems, and each is illustrated (Pl. 8, p. 70) by figures of the wings of *Aeshna canadensis* Walk.

In taxonomic matters there are some innovations, but in general these are subordinate, as might be expected in a group in which the systematic arrangement is relatively stable as a result of much previous careful work. However, the author's views on the subgeneric categories of the genus *Gomphus* s.l. based on his recent studies of male genitalic structures are a notable contribution toward a better understanding of this taxonomically difficult group. Also, in other groups he often gives additional information that clarifies the relationships of certain species or reinforces their previously proposed synonymies. In such matters there is everywhere apparent his keen appreciation of the need for the integration of morphological, ecological and behavioristic data in the definition of species. In this volume, as in the preceding, no new species are introduced, and except for the division into two subspecies of the well-known species, *Gomphus fraternus* (Say), requiring the proposal of the new trinomen, *Gomphus fraternus manitobanus*, there are no subspecific novelties. It is perhaps an oversight that the author has failed to designate a holotype for this subspecies, a matter which, however, can be taken care of in his next volume.

Distributionwise, the volume contains much new information. The known ranges of several species are considerably extended, especially by new northern records, the ranges of some species(e.g. *Aeshna umbrosa* Walk.) are redefined, and attention is directed to certain anomalies in distribution (notably in the distribution of *Aeshna tuberculifera* Walk., which in addition to being recorded from "N.S. to Wis., s. to R.I., Conn., Pa. and Ind." is also reported from "w.B.C."). On the other hand the paucity of Canadian records for some species (e.g., *Gomphus viridifrons* Hine and *G. plagiatus* Selys) points to the need for further collecting.

The work concludes with a bibliography and an index.

The present volume bears the same indelible stamp of quality that is characteristic of the other writings of the author. It is erudite, and scholarly, yet withal it is infused with a freshness and vitality that reveal the author's deep affection for his subject – an affection that, perhaps, is a factor greater than any other in persuading him, in his advancing years, to devote his energies to the completion of this work.

G. Stuart Walley

The Components of Predation as Revealed by a Study of Small-Mammal Predation of the European Pine Sawfly[1]

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INTRODUCTION

The fluctuation of an animal's numbers between restricted limits is determined by a balance between that animal's capacity to increase and the environmental checks to this increase. Many authors have indulged in the whimsy of calculating the progressive increase of a population when no checks were operating. Thus Huxley calculated that the progeny of a single *Aphis* in the course of 10 generations, supposing all survived, would "contain more ponderable substance than five hundred millions of stout men; that is, more than the whole population of China", (in Thompson, 1929). Checks, however, do occur and it has been the subject of much controversy to determine how these checks operate. Certain general principles—the density-dependence concept of Smith (1955), the competition theory of Nicholson (1933)—have been proposed both verbally and mathematically, but because they have been based in part upon untested and restrictive assumptions they have been severely criticized (e.g. Andrewartha and Birch 1954). These problems could be considerably clarified if we knew the mode of operation of each process that affects numbers, if we knew its basic and subsidiary components. Predation, one such process, forms the subject of the present paper.

Many of the published studies of predation concentrate on discrete parts rather than the whole process. Thus some entomologists are particularly interested in the effect of selection of different kinds of prey by predators upon the evolution of colour patterns and mimicry; wildlife biologists are similarly interested in selection but emphasize the role predators play in improving the condition of the prey populations by removing weakened animals. While such specific problems should find a place in any scheme of predation, the main aim of the present study is to elucidate the components of predation in such a way that more meaning can be applied to considerations of population dynamics. This requires a broad study of the whole process and in particular its function in affecting the numbers of animals.

Such broad studies have generally been concerned with end results measured by the changes in the numbers of predator and prey. These studies are particularly useful when predators are experimentally excluded from the environment of their prey, in the manner adopted by DeBach and his colleagues in their investigations of the pests of orchard trees in California. This work, summarized recently (DeBach, 1958) in response to criticism by Milne (1957), clearly shows that in certain cases the sudden removal of predators results in a rapid increase of prey numbers from persistently low densities to the limits of the food supply. Inasmuch as these studies have shown that other factors have little regulatory function, the predators appear to be the principal ones responsible for regulation. Until the components of predation are revealed by an analysis of the processes leading to these end results, however, we will never know whether the conclusions from such studies apply to situations other than the specific predator–prey relationship investigated.

Errington's investigations of vertebrate predator–prey situations (1934, 1943, 1945 and 1956) suggest, in part, how some types of predation operate. He has

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postulated that each habitat can support only a given number of animals and that predation becomes important only when the numbers of prey exceed this "carrying capacity". Hence predators merely remove surplus animals, ones that would succumb even in the absence of natural enemies. Errington exempts certain predator-prey relations from this scheme, however, and quotes the predation of wolves on deer as an example where predation probably is not related to the carrying capacity of the habitat. However logical these postulates are, they are only indirectly supported by the facts, and they do not explain the processes responsible.

In order to clarify these problems a comprehensive theory of predation is required that on the one hand is not so restrictive that it can only apply in certain cases and on the other not so broad that it becomes meaningless. Such a comprehensive answer requires a comprehensive approach, not necessarily in terms of the number of situations examined but certainly in terms of the variables involved, for it is the different reactions of predators to these variables that produce the many diverse predator-prey relations. Such a comprehensive approach is faced with a number of practical difficulties. It is apparent from the published studies of predation of vertebrate prey by vertebrate predators that not only is it difficult to obtain estimates of the density of predator, prey, and destroyed prey, but also that the presence of many interacting variables confuses interpretation.

The present study of predation of the European pine sawfly, *Neodiprion sertifer* (Geoff.) by small mammals was particularly suited for a general comprehensive analysis of predation. The practical difficulties concerning population measurement and interpretation of results were relatively unimportant, principally because of the unique properties of the environment and of the prey. The field work was conducted in the sand-plain area of southwestern Ontario where Scots and jack pine have been planted in blocks of up to 200 acres. The flat topography and the practice of planting trees of the same age and species at standard six-foot spacings has produced a remarkably uniform environment. In addition, since the work was concentrated in plantations 15 to 20 years of age, the closure of the crowns reduced ground vegetation to a trace, leaving only an even layer of pine needles covering the soil. The extreme simplicity and uniformity of this environment greatly facilitated the population sampling and eliminated complications resulting from changes in the quantity and kind of alternate foods of the predators.

The investigations were further simplified by the characteristics of the prey. Like most insects, the European pine sawfly offers a number of distinct life-history stages that might be susceptible to predation. The eggs, laid in pine needles the previous fall, hatch in early spring and the larvae emerge and feed upon the foliage. During the first two weeks of June the larvae drop from the trees and spin cocoons within the duff on the forest floor. These cocooned sawflies remain in the ground until the latter part of September, when most emerge as adults. A certain proportion, however, overwinter in cocoons, to emerge the following autumn. Observations in the field and laboratory showed that only one of these life-history stages, the cocoon, was attacked by the small-mammal predators, and that the remaining stages were inacessible and/or unpalatable and hence completely escaped attack. These data will form part of a later paper dealing specifically with the impact of small mammal predation upon the European pine sawfly.

Cocooned sawflies, as prey, have some very useful attributes for an investigation of this kind. Their concentration in the two-dimensional environment of the duff-soil interface and their lack of movement and reaction to predators considerably simplify sampling and interpretation. Moreover, the small mammals'

habit of making a characteristically marked opening in the cocoon to permit removal of the insect leaves a relatively permanent record in the ground of the number of cocooned sawflies destroyed. Thus, the density of the destroyed prey can be measured at the same time as the density of the prey.

Attention was concentrated upon the three most numerous predators—the masked shrew, *Sorex cinereus cinereus* Kerr, the short-tail shrew, *Blarina brevicauda talpoides* Gapper, and deer mouse, *Peromyscus maniculatus bairdii* Hoy and Kennicott. It soon became apparent that these species were the only significant predators of the sawfly, for the remaining nine species trapped or observed in the plantations were either extremely rare or were completely herbivorous.

Here, then, was a simple predator-prey situation where three species of small mammals were preying on a simple prey—sawfly cocoons. The complicating variables present in most other situations were either constant or absent because of the simple characteristics of the environment and of the prey. The absence or constancy of these complicating variables facilitated analysis but at the expense of a complete and generally applicable scheme of predation. Fortunately, however, the small-mammal predators and the cocoons could easily be manipulated in laboratory experiments so that the effect of those variables absent in the field situation could be assessed. At the same time the laboratory experiments supported the field results. This blend of field and laboratory data provides a comprehensive scheme of predation which will be shown to modify present theories of population dynamics and to considerably clarify the role predators play in population regulation.

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FIELD TECHNIQUES

A study of the interaction of predator and prey should be based upon accurate population measurements, and in order to avoid superficial interpretations, populations should be expressed as numbers per unit area. Three populations must be measured—those of the predators, prey, and destroyed prey. Thus the aim of the field methods was to measure accurately each of the three populations in terms of their numbers per acre.

Small-Mammal Populations

Since a complete description and evaluation of the methods used to estimate the density of the small-mammal predators forms the basis of another paper in preparation, a summary of the techniques will suffice for the present study.

Estimates of the number of small mammals per acre were obtained using standard live-trapping techniques adapted from Burt (1940) and Blair (1941). The data obtained by marking, releasing and subsequently recapturing animals were analysed using either the Lincoln index (Lincoln, 1930) or Hayne's method for estimating populations in removal trapping procedures (Hayne, 1949). The resulting estimates of the number of animals exposed to traps were converted to per acre figures by calculating, on the basis of measurements of the home range of the animals (Stickel, 1954), the actual area sampled by traps.

The accuracy of these estimates was evaluated by examining the assumptions underlying the proper use of the Lincoln index and Hayne's technique and by comparing the efficiency of different traps and trap arrangements. This analysis showed that an accurate estimate of the numbers of *Sorex* and *Blarina* could be

obtained using Hayne's method of treating the data obtained from trapping with bucket traps. These estimates, however, were accurate only when the populations had not been disturbed by previous trapping. For *Peromyscus*, Lincoln-index estimates obtained from the results of trapping with Sherman traps provided an ideal way of estimating numbers that was both accurate and unaffected by previous trapping.

N. sertifer Populations

Since small-mammal predation of *N. sertifer* was restricted to the cocoon stage, prey populations could be measured adequately by estimating the number of cocoons containing living insects present immediately after larval drop in June. This estimate was obtained using a method outlined and tested by Prebble (1943) for cocoon populations of the European spruce sawfly, *Gilpinia hercyniae* (Htg.), an insect with habits similar to those of *N. sertifer*. Accurate estimates were obtained when cocoons were collected from sub-samples of litter and duff distributed within the restricted universe beneath the crowns of host trees. This method was specially designed to provide an index of population rather than an estimate of numbers per acre. But it is obvious from this work that any cocoon-sampling technique designed to yield a *direct* estimate of the number of cocoons per acre would require an unpractically large number of sample units. It proved feasible in the present study, however, to convert such estimates from a square-foot to an acre basis, by stratifying the forest floor into three strata, one comprising circles with two-foot radii around tree trunks, one comprising intermediate rings with inner radii two feet and outer radii three feet, and one comprising the remaining area (three to five feet from the tree trunks).

At least 75 trees were selected and marked throughout each plantation, and one or usually two numbered wooden stakes were placed directly beneath the crown of each tree, on opposite sides of the trunk. Stakes were never placed under overlapping tree crowns. The four sides of each stake were lettered from A to D and the stake was placed so that the numbered sides bore no relation to the position of the trunk. Samples were taken each year, by collecting cocoons from the area delimited by one-square-foot frames placed at one corner of each stake. In the first year's sample the frames were placed at the AB corner, in the second year's at the BC corner, etc. Different-sized screens were used to separate the cocoons from the litter and duff.

Cocoons were collected in early September before adult sawflies emerged and those from each quadrat were placed in separate containers for later analysis. These cocoons were analysed by first segregating them into "new" and "old" categories. Cocoons of the former category were a bright golden colour and were assumed to have been spun in the year of sampling, while those of the latter were dull brown in colour and supposedly had been spun before the sampling year. These assumptions proved partly incorrect, however, for some of the cocoons retained their new colour for over one year. Hence the "new" category contained enough cocoons that had been spun before the sampling year to prevent its use, without correction, as an estimate of the number of cocoons spun in the year of sampling. A correction was devised, however, which reduced the error to negligible proportions.

This method provided the best available estimate of the number of healthy cocoons per acre present in any one year. The population figures obtained ranged from 39,000 (Plot 1, 1954) to 1,080,000 (Plot 2, 1952) cocoons per acre.

Predation

Small-mammal predation has a direct and indirect effect on *N. sertifer* populations. The direct effect of predation is studied in detail in this paper. The

indirect effect, resulting from the mutual interaction of various control factors (parasites, disease, and predators) has been discussed in previous papers (Holling, 1955, 1958b).

The direct effect of predation was measured in a variety of ways. General information was obtained from studies of the consumption of insects by caged animals and from the analysis of stomach contents obtained from animals trapped in sawfly-infested plantations. More particular information was obtained from the analysis of cocoons collected in the regular quadrat samples and from laboratory experiments which studied the effect of cocoon density upon predation.

The actual numbers of *N. sertifer* cocoons destroyed were estimated from cocoons collected in the regular quadrat samples described previously. As shown in an earlier paper (Holling, 1955), cocoons opened by small mammals were easily recognized and moreover could be classified as to species of predator. These estimates of the number of new and old cocoons per square foot opened by each species of predator were corrected, as before, to provide an estimate of the number opened from the time larvae dropped to the time when cocoon samples were taken in early September.

It has proved difficult to obtain a predation and cocoon-population estimate of the desired precision and accuracy. The corrections and calculations that had to be applied to the raw sampling data cast some doubt upon the results and conclusions based upon them. It subsequently developed, however, that a considerable margin of error could be tolerated without changing the results and the conclusions that could be derived from them. In any case, all conclusions based upon cocoon-population estimates were supported and substantiated by results from controlled laboratory experiments.

LABORATORY TECHNIQUES

Several experiments were conducted with caged animals in order to support and expand results obtained in the field. The most important of these measured the number of cocoons consumed by *Peromyscus* at different cocoon densities. These experiments were conducted at room temperature (ca. 20°C) in a screen-topped cage, 10′ x 4′ x 6″. At the beginning of an experiment, cocoons were first buried in sand where the lines of a removable grid intersected, the grid was then removed, the sand was pressed flat, and a metal-edged levelling jig was finally scraped across the sand so that an even 12 mm. covered the cocoons. A single deer mouse was then placed in the cage together with nesting material, water, and an alternate food—dog biscuits. In each experiment the amount of this alternate food was kept approximately the same (i.e. 13 to 17 gms. dry weight). After the animal had been left undisturbed for 24 hours, the removable grid was replaced, and the number of holes dug over cocoons, the number of cocoons opened and the dry weight of dog biscuits eaten were recorded. Consumption by every animal was measured at either four or five different densities ranging from 2.25 to 36.00 cocoons per sq. ft. The specific densities were provided at random until all were used, the consumption at each density being measured for three to six consecutive days. Ideally the size of the cage should remain constant at all densities but since this would have required over 1,400 cocoons at the highest density, practical considerations necessitated a compromise whereby the cage was shortened at the higher densities. In these experiments the total number of cocoons provided ranged from 88 at the lowest density to 504 at the highest. At all densities, however, these numbers represented a surplus and no more than 40 per cent were ever consumed in a single experiment. Hence consumption was not limited by shortage of cocoons, even though the size of the cage changed.

The sources and characteristics of the cocoons and *Peromyscus* used in these experiments require some comment. Supplies of the prey were obtained by collecting cocoons in sawfly-infested plantations or by collecting late-instar larvae and allowing them to spin cocoons in boxes provided with foliage and litter. Sound cocoons from either source were then segregated into those containing healthy, parasitized, and diseased prepupae using a method of X-ray analysis (Holling, 1958a). The small male cocoons were separated from the larger female cocoons by size, since this criterion had previously proved adequate (Holling, 1958b). To simplify the experiments, only male and female cocoons containing healthy, living prepupae were used and in each experiment equal numbers of cocoons of each sex were provided, alternately, in the grid pattern already described.

Three mature non-breeding male deer mice were used in the experiments. Each animal had been born and raised in small rearing cages 12 x 8 x 6 in. and had been isolated from cocoons since birth. They therefore required a period to become familiar with the experimental cage and with cocoons. This experience was acquired during a preliminary three-week period. For the first two weeks the animal was placed in the experimental cage together with nesting material, water, dog biscuits and sand, and each day was disturbed just as it would be if an experiment were in progress. For the final week cocoons were buried in the sand at the first density chosen so that the animal could learn to find and consume the cocoon contents. It has been shown (Holling, 1955, 1958b) that a seven-day period is more than ample to permit complete learning.

THE COMPONENTS OF PREDATION

A large number of variables could conceivably affect the mortality of a given species of prey as a result of predation by a given species of predator. These can conveniently be classified, as was done by Leopold (1933), into five groups:

(1) density of the prey population.
(2) density of the predator population.
(3) characteristics of the prey, e.g., reactions to predators, stimulus detected by predator, and other characteristics.
(4) density and quality of alternate foods available for the predator.
(5) characteristics of the predator, e.g., food preferences, efficiency of attack, and other characteristics.

Each of these variables may exert a considerable influence and the effect of any one may depend upon changes in another. For example, Errington (1946) has shown that the characteristics of many vertebrate prey species change when their density exceeds the number that the available cover can support. This change causes a sudden increase in predation. When such complex interactions are involved, it is difficult to understand clearly the principles involved in predation; to do so we must find a simplified situation where some of the variables are constant or are not operating. The problem studied here presents such a situation. First, the characteristics of cocoons do not change as the other factors vary and there are no reactions by the cocooned sawflies to the predators. We therefore can ignore, temporarily, the effect of the third factor, prey characteristics. Secondly, since the work was conducted in plantations noted for their uniformity as to species, age, and distribution of trees, there was a constant and small variety of possible alternate foods. In such a simple and somewhat sterile environment, the fourth factor, the density and quality of alternate foods, can therefore be initially ignored, as can the fifth factor, characteristics of the predator, which is really only another way of expressing factors three and four. There are thus only two

basic variables affecting predation in this instance, i.e., prey density and predator density. Furthermore, these are the only essential ones, for the remainder, while possibly important in affecting the amount of predation, are not essential to describe its fundamental characteristics.

The Basic Components

It is from the two essential variables that the basic components of predation will be derived. The first of these variables, prey density, might affect a number of processes and consumption of prey by individual predators might well be one of them.

The data which demonstrate the effect of changes of prey density upon consumption of cocooned sawflies by *Peromyscus* were obtained from the yearly cocoon quadrat samples in Plots 1 and 2. In 1951, Dr. F. T. Bird, Laboratory of Insect Pathology, Sault Ste. Marie, Ont., had sprayed each of these plots with a low concentration of a virus disease that attacked *N. sertifer* larvae, (Bird 1953). As a result, populations declined from 248,000 and 1,080,000 cocoons per acre, respectively, in 1952, to 39,000 and 256,000 in 1954. Thus predation values at six different cocoon densities were obtained. An additional sample in a neighbouring plantation in 1953 provided another value.

Predation values for *Sorex* and *Blarina* were obtained from one plantation, Plot 3, in one year, 1952. In the spring of that year, virus, sprayed from an aircraft flying along parallel lines 300 feet apart, was applied in three concentrations, with the lowest at one end of the plantation and the highest at the other. An area at one end, not sprayed, served as a control. When cocoon populations were sampled in the autumn, a line of 302 trees was selected at right angles to the lines of spray and the duff under each was sampled with one one-square-foot quadrat. The line, approximately 27 chains long, ran the complete length of the plantation. When the number of new cocoons per square foot was plotted against distance, discrete areas could be selected which had fairly constant populations that ranged from 44,000 to 571,000 cocoons per acre. The areas of low population corresponded to the areas sprayed with the highest concentration of virus. In effect, the plantation could be divided into rectangular strips, each with a particular density of cocoons. The width of these strips varied from 126 to 300 feet with an average of 193 feet. In addition to the 302 quadrats examined, the cocoons from another 100 quadrats were collected from the areas of lowest cocoon densities. Thus, in this one plantation in 1952, there was a sufficient number of different cocoon densities to show the response of consumption by *Sorex* and *Blarina* to changes of prey density.

The methods used to estimate predator densities in each study plot require some further comment. In Plots 1 and 2 this was done with grids of Sherman traps run throughout the summer. In Plot 3 both a grid of Sherman traps and a line of snap traps were used. This grid, measuring 18 chains by 4 chains, was placed so that approximately the same area sampled for cocoons was sampled for small mammals. The populations determined from these trapping procedures were plotted against time, and the number of "mammal-days" per acre, from the start of larval drop (June 14) to the time cocoon samples were made (Aug. 20-30), was determined for each plot each year. This could be done with *Peromyscus* and *Blarina* since the trapping technique was shown to provide an accurate estimate of their populations. But this was not true for *Sorex*. Instead, the number of *Sorex*-days per acre was approximated by dividing the number of cocoons opened at the highest density by the known number consumed by caged *Sorex* per day, i.e. 101. Since the number of cocoons opened at the highest cocoon density was

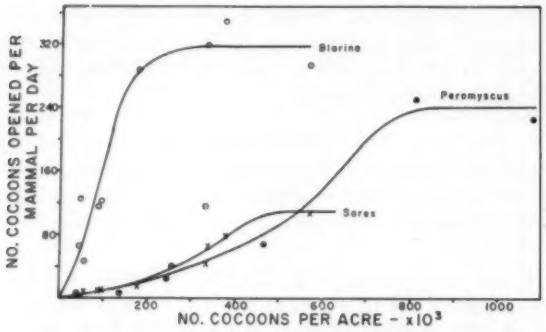

Fig. 1. Functional responses of *Blarina*, *Sorex* and *Peromyscus* in plots 1, 2, and 3.

151,000 per acre, then the number of *Sorex*-days per acre should be 151,000/101 = 1,490. This is approximately 10 times the estimate that was obtained from trapping with Sherman traps. When the various trapping methods were compared, estimates from Sherman trapping were shown to underestimate the numbers of *Sorex* by about the same amount, i.e. one-tenth.

With estimates of the numbers of predators, prey and destroyed prey available, the daily number of prey consumed per predator at different cocoon densities can be calculated. As seen in Fig. 1, the number of cocoons opened by each species increased with increasing cocoon density until a maximum daily consumption was reached that corresponded approximately to the maximum number that could be consumed in any one day by caged animals. For *Sorex* this of course follows from the method of calculation. The rates at which these curves rise differ for the different species, being greatest for *Blarina* and least for *Peromyscus*. Even if the plateaus are equated by multiplying points on each curve by a constant, the rates still decrease in the same order, reflecting a real difference in species behaviour.

The existence of such a response to cocoon density may also be demonstrated by data from the analysis of stomach contents. The per cent occurrence and per cent volume of the various food items in stomachs of *Peromyscus* captured immediately after larval drop and two months later is shown in Table I. When cocoon densities were high, immediately after larval drop, the per cent occurrence and per cent volume of *N. sertifer* material was high. Two months later when various cocoon mortality factors had taken their toll, cocoon densities were lower and

TABLE I

Stomach contents of *Peromyscus* trapped immediately before larval drop and two months later

Time trapped	Approx. no. cocoons per acre	No. of stomachs	Analysis	Plant	*N. sertifer*	Other insects	All insects
June 16–21	600,000	19	% occurrence	37%	95%	53%	100%
Aug. 17–19	300,000	14		79%	50%	64%	86%
June 16–21	600,000	19	% volume	5%	71%	24%	95%
Aug. 17–19	300,000	14		47%	19%	34%	53%

TABLE II

Occurrence of food items in stomachs of *Microtus* trapped before and after larval drop

Time trapped	Plant		*N. sertifer*		All insects	
	No. of stomachs	% occurrence	No. of stomachs	% occurrence	No. of stomachs	% occurrence
before larval drop	25	100%	2	8%	2	8%
after larval drop	29	100%	8	28%	11	38%

N. sertifer was a less important food item. The decrease in consumption of *N. sertifer* was accompanied by a considerable increase in the consumption of plant material and a slight increase in the consumption of other insect material. Plants and other insects acted as buffer or alternate foods. *Microtus*, even though they ate few non-plant foods in nature, also showed an increase in the per cent occurrence of *N. sertifer* material in stomachs as cocoon density increased (Table II). Before larval drop, when cocoon densities were low, the incidence of *N. sertifer* in *Microtus* stomachs was low. After larval drop, when cocoon densities were higher, the incidence increased by 3.5 times. Even at the higher cocoon densities, however, *N. sertifer* comprised less than one per cent of the volume of stomach contents so that this response to changes in prey density by *Microtus* is extremely low.

The graphs presented in Fig. I and the results of the analyses of stomach contents leave little doubt that the consumption of cocooned sawflies by animals in the field increases with increase in cocoon density. Similar responses have been demonstrated in laboratory experiments with three *Peromyscus*. As shown in Fig. 2, the number of cocoons consumed daily by each animal increased with increase in cocoon density, again reaching a plateau as did the previous curves. Whenever the number of prepupae consumed did not meet the caloric requirements, these were met by consumption of the dog biscuits, the alternate food provided. Only one of the animals (A) at the highest density fulfilled its caloric requirements by consuming prepupae; the remaining animals (B and C) consumed

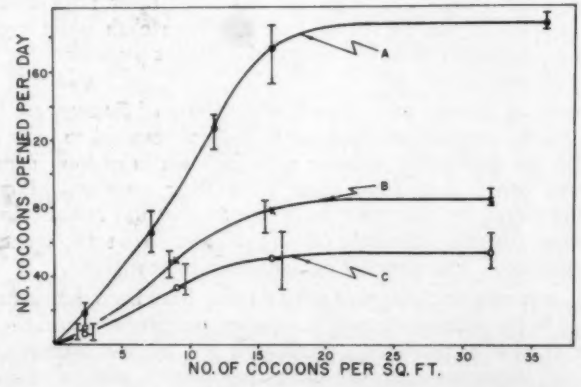

Fig. 2. Functional responses of three caged *Peromyscus* (means and ranges shown).

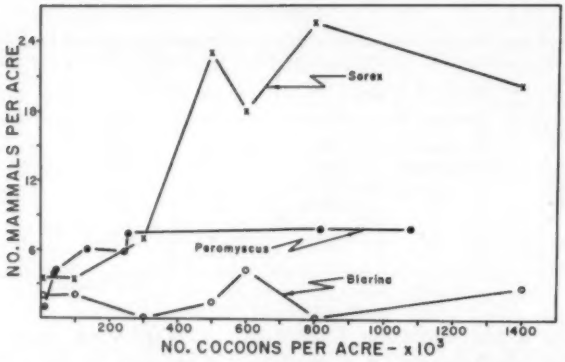

Fig. 3. Numerical responses of *Blarina, Sorex* and *Peromyscus.*

less than one-half the number of sawflies they would consume if no alternate foods were present. The cocoons used in experiments involving animals B and C, however, had been spun 12 months earlier than those involving animal A. When the characteristics of the functional response are examined in another paper, it will be shown that the strength of stimulus from older cocoons is less than that from younger cocoons, and that these differences are sufficient to explain the low consumption by animals B and C. The shape of the curves and the density at which they level is very similar for all animals, so similar that multiplying points along any one curve by the proper constant will equate all three. These curves are very similar to the ones based upon field data. All show the same form, the essential feature of which is an S-shaped rise to a plateau.

The effect of changes of prey density need not be restricted exclusively to consumption of prey by individual predators. The density of predators may also be affected and this can be shown by relating the number of predators per acre to the number of cocoons per acre. Conclusions can be derived from these relations but they are tentative. The data were collected over a relatively short period of time (four summers) and thus any relationship between predator numbers and prey density may have been fortuitous. Only those data obtained in plantations over 12 years old are included since small mammal populations were most stable in these areas. The data for the three most important species of predators are shown in the curves of Fig. 3, where each point represents the highest summer population observed either in different plantations or in the same plantation in different years.

The densities of *Blarina* were lowest while those of *Sorex* were highest. In this situation, *Blarina* populations apparently did not respond to prey density, for its numbers did not noticeably increase with increase in cocoon density. Some agent or agents other than food must limit their numbers. Populations of *Peromyscus* and *Sorex*, on the other hand, apparently did initially increase with increase in cocoon density, ultimately ceasing to increase as some agents other than food became limiting. The response of *Sorex* was most marked.

Thus two responses to changes of prey density have been demonstrated. The first is a change in the number of prey consumed per predator and the second is a change in the density of predators. Although few authors appear to recognize the existence and importance of *both* these responses to changes of prey density, they have been postulated and, in the case of the change of predator density,

demonstrated. Thus Solomon (1949) acknowledged the two-fold nature of the response to changes of prey density, and applied the term *functional response* to the change in the number of prey consumed by individual predators, and the term *numerical response* to the change in the density of predators. These are apt terms and, although they have been largely ignored in the literature, they will be adopted in this paper. The data available to Solomon for review did not permit him to anticipate the form the functional response of predators might take, so that he could not assess its importance in population regulation. It will be shown, however, that the functional response is as important as the numerical.

It remains now to consider the effect of predator density, the variable that, together with prey density, is essential for an adequate description of predation. Predator density might well affect the number of prey consumed per predator. Laboratory experiments were designed to measure the number of cocoons opened by one, two, four, and eight animals in a large cage provided with cocoons at a density of 15 per square foot and a surplus of dog biscuits and water. The average number of cocoons opened per mouse in eight replicates was 159, 137, 141 and 159 respectively. In this experiment, therefore, predator density apparently did not greatly affect the consumption of prey by individual animals. This conclusion is again suggested when field and laboratory data are compared, for the functional response of *Peromyscus* obtained in the field, where its density varied, was very similar to the response of single animals obtained in the laboratory.

In such a simple situation, where predator density does not greatly affect the consumption by individuals, the total predation can be expressed by a simple, additive combination of the two responses. For example, if at a particular prey density the functional response is such that 100 cocoons are opened by a single predator in one day, and the numerical response is such that the predator density is 10, then the total daily consumption will be simply 100 x 10. In other situations, however, an increase in the density of predators might result in so much competition that the consumption of prey by individual predators might drop significantly. This effect can still be incorporated in the present scheme by adopting a more complex method of combining the functional and numerical responses.

This section was introduced with a list of the possible variables that could affect predation. Of these, only the two operating in the present study – prey and predator density – are essential variables, so that the basic features of predation can be ascribed to the effects of these two. It has been shown that there are two responses to prey density. The increase in the number of prey consumed per predator, as prey density rises, is termed the functional response, while the change in the density of predators is termed the numerical response. The total amount of predation occurring at any one density results from a combination of the two responses, and the method of combination will be determined by the way predator density affects consumption. This scheme, therefore, describes the effects of the basic variables, uncomplicated by the effects of subsidiary ones. Hence the two responses, the functional and numerical, can be considered the basic components of predation.

The total amount of predation caused by small mammals is shown in Fig. 4, where the functional and numerical responses are combined by multiplying the number of cocoons opened per predator at each density by the number of effective mammal-days observed. These figures were then expressed as percentages opened. This demonstrates the relation between per cent predation and prey density during the 100-day period between cocoon formation and adult emergence. Since the data obtained for the numerical responses are tentative, some reservations must be applied to the more particular conclusions derived

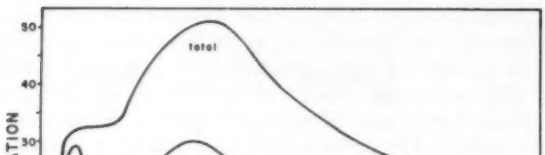

Fig. 4. Functional and numerical responses combined to show the relation between per cent predation and cocoon density.

from this figure. The general conclusion, that per cent predation by each species shows an initial rise and subsequent decline as cocoon density increases holds, however. For this conclusion to be invalid, the numerical responses would have to decrease in order to mask the initial rise in per cent predation caused by the S-shaped form of the functional responses. Thus from zero to some finite cocoon density, predation by small mammals shows a direct density-dependent action and thereafter shows an inverse density-dependent action. The initial rise in the proportion of prey destroyed can be attributed to both the functional and numerical responses. The functional response has a roughly sigmoid shape and hence the proportion of prey destroyed by an individual predator will increase with increase in cocoon density up to and beyond the point of inflection. Unfortunately the data for any one functional response curve are not complete enough to establish a sigmoid relation, but the six curves presented thus far and the several curves to be presented in the following section all suggest a point of inflection. The positive numerical responses shown by *Sorex* and *Peromyscus* also promote a direct density-dependent action up to the point at which predator densities remain constant. Thereafter, with individual consumption also constant, the per cent predation will decline as cocoon density increases. The late Dr. L. Tinbergen apparently postulated the same type of dome-shaped curves for the proportion of insects destroyed by birds. His data were only partly published (1949, 1955) before his death, but Klomp (1956) and Voûte (1958) have commented upon the existence of these "optimal curves". This term, however, is unsatisfactory and anthropocentric. From the viewpoint of the forest entomologist, the highest proportion of noxious insects destroyed may certainly be the optimum, but the term is meaningless for an animal that consumes individuals and not percentages. Progress can best be made by considering predation first as a behaviour before translating this behaviour in terms of the proportion of prey destroyed. The term "peaked curve" is perhaps more accurate.

Returning to Fig. 4, we see that the form of the peaked curve for *Blarina* is determined solely by the functional response since this species exhibited no numerical response. The abrupt peak occurs because the maximum consumption of prepupae was reached at a very low prey density before the predation was "diluted" by large numbers of cocoons. With *Sorex* both the numerical and functional responses are important. Predation by *Sorex* is greatest principally because of the marked numerical response. The two responses again determine

the form of the peaked curve for *Peromyscus*, but the numerical response, unlike that of *Sorex*, was not marked, and the maximum consumption of cocoons was reached only at a relatively high density; the result is a low per cent predation with a peak occurring at a high cocoon density.

Predation by all species destroyed a considerable number of cocooned sawflies over a wide range of cocoon densities. The presence of more than one species of predator not only increased predation but also extended the range of prey densities over which predation was high. This latter effect is particularly important, for if the predation by several species of predators peaked at the same prey density the range of densities over which predation was high would be slight and if the prey had a sufficiently high reproductive capacity its density might jump this vulnerable range and hence escape a large measure of the potential control that could be exerted by predators. Before we can proceed further in the discussion of the effect of predation upon prey numbers, the additional components that make up the behaviour of predation must be considered.

The Subsidiary Components

Additional factors such as prey characteristics, the density and quality of alternate foods, and predator characteristics have a considerable effect upon predation. It is necessary now to demonstrate the effect of these factors and how they operate.

There are four classes of prey characteristics: those that influence the caloric value of the prey; those that change the length of time prey are exposed; those that affect the "attractiveness" of the prey to the predator (e.g. palatability, defence mechanisms); and those that affect the strength of stimulus used by predators in locating prey (e.g. size, habits, and colours). Only those characteristics that affect the strength of stimulus were studied experimentally. Since small mammals detect cocoons by the odour emanating from them (Holling, 1958b), the strength of this odour perceived by a mammal can be easily changed in laboratory experiments by varying the depth of sand covering the cocoons.

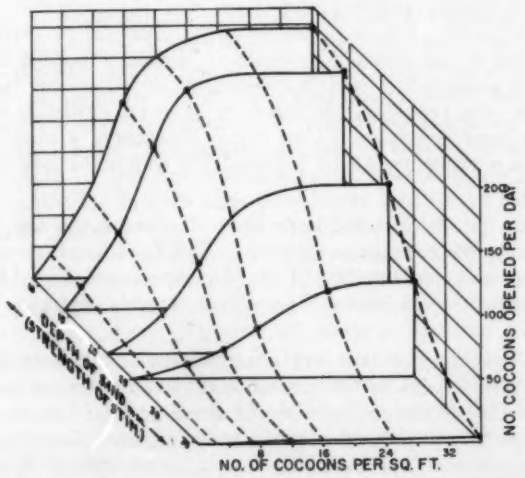

Fig. 5. Effect of strength of stimulus from cocoons upon the functional response of one caged *Peromyscus*. Each point represents the average of three to six replicates.

One *Peromyscus* was used in these experiments and its daily consumption of cocoons was measured at different cocoon densities and different depths of sand. These data are plotted in Fig. 5. Since the relation between depth of sand and strength of stimulus must be an inverse one, the depths of sand are reversed on the axis so that values of the strength of stimulus increase away from the origin. Each point represents the mean of three to six separate measurements. Decreasing the strength of the perceived stimulus by increasing the depth of sand causes a marked decrease in the functional response. A 27 mm. increase in depth (from nine to 36 mm.), for example, causes the peak consumption to drop from 196 to four cocoons per day. The daily number of calories consumed in all these experiments remained relatively constant since dog biscuits were always present as alternate food. The density at which each functional-response curve levels appear to increase somewhat as the strength of stimulus perceived by the animal decreases. We might expect that the increase in consumption is directly related to the increase in the proportion of cocoons in the amount of food available, at least up to the point where the caloric requirements are met solely by sawflies. The ascending portions of the curves, however, are S-shaped and the level portions are below the maximum consumption, approximately 220 cocoons for this animal. Therefore, the functional response cannot be explained by random searching for cocoons. For the moment, however, the important conclusion is that changes in prey characteristics can have a marked effect on predation but this effect is exerted through the functional response.

In the plantations studied, cocoons were not covered by sand but by a loose litter and duff formed from pine needles. Variations in the depth of this material apparently did not affect the strength of the perceived odour, for as many cocoons were opened in quadrats with shallow litter as with deep. This material must be so loose as to scarcely impede the passage of odour from cocoons.

The remaining subsidiary factors, the density and quality of alternate foods and predator characteristics, can also affect predation. The effect of alternate foods could not be studied in the undisturbed plantations because the amount of these "buffers" was constant and very low. The effect of quality of alternate foods on the functional response, however, was demonstrated experimentally using one *Peromyscus*. The experiments were identical to those already described except that at one series of densities an alternate food of low palatability (dog biscuits) was provided, and at the second series one of high palatability (sunflower seeds) was provided. When both foods are available, deer mice select sunflower seeds over dog biscuits. In every experiment a constant amount of alternate food was available: 13 to 17 gms. dry weight of dog biscuits, or 200 sunflower seeds.

Fig. 6 shows the changes in the number of cocoons opened per day and in the amount of alternate foods consumed. The functional response decreased with an increase in the palatability of the alternate food (Fig. 6A). Again the functional response curves showed an initial, roughly sigmoid rise to a constant level.

As cocoon consumption rose, the consumption of alternate foods decreased (Fig. 6B) at a rate related to the palatability of the alternate food. Each line indicating the change in the consumption of alternate food was drawn as a mirror image of the respective functional response and these lines closely follow the mean of the observed points. The variability in the consumption of sunflower seeds at any one cocoon density was considerable, probably as a result of the extreme variability in the size of seeds.

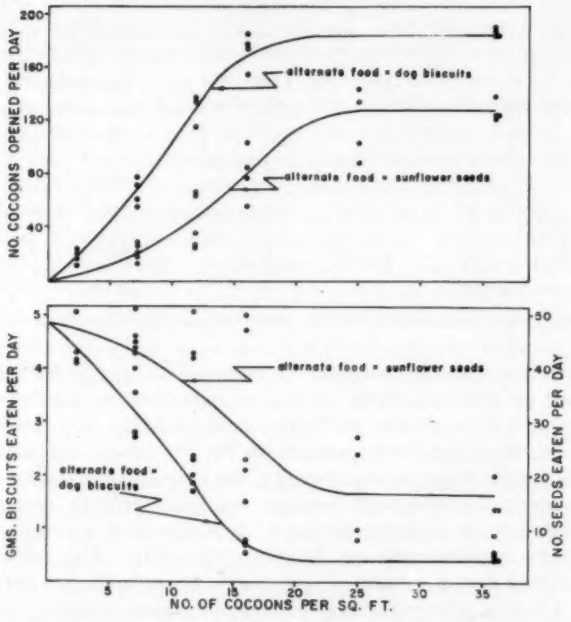
NO. COCOONS OPENED PER DAY
alternate food = dog biscuits
alternate food = sunflower seeds
GMS. BISCUITS EATEN PER DAY
NO. SEEDS EATEN PER DAY
alternate food = sunflower seeds
alternate food = dog biscuits
NO. OF COCOONS PER SQ. FT.

Fig. 6. Effect of different alternate foods upon the functional response of one *Peromyscus*. *A* (upper) shows the functional responses when either a low (dog biscuits) or a high (sunflower seeds) palatability alternate food was present in excess. *B* (lower) shows the amount of these alternate foods consumed.

Again we see that there is not a simple relation between the number of cocoons consumed and the proportion of cocoons in the total amount of food available. This is most obvious when the functional response curves level, for further increase in density is not followed by an increase in the consumption of sawflies. The plateaus persist because the animal continued consuming a certain fixed quantity of alternate foods. L. Tinbergen (1949) observed a similar phenomenon in a study of predation of pine-eating larvae by tits in Holland. He presented data for the consumption of larvae of the pine beauty moth, *Panolis griseovariegata*, and of the web-spinning sawfly *Acantholyda pinivora*, each at two different densities. In each case more larvae were eaten per nestling tit per day at the higher prey density. This, then, was part of a functional response, but it was that part above the point of inflection, since the proportion of prey eaten dropped at the higher density. It is not sufficient to explain these results as well as the ones presented in this paper by claiming, with Tinbergen, that the predators "have the tendency to make their menu as varied as possible and therefore guard against one particular species being strongly dominant in it". This is less an explanation than an anthropocentric description. The occurrence of this phenomenon depends upon the strength of stimulus from the prey, and the amount and quality of the alternate foods. Its proper explanation must await the collection of further data.

We now know that the palatability of alternate foods affects the functional response. Since the number of different kinds of alternate food could also have

TABLE III

The effect of alternate foods upon the number of cocoons consumed per day by one *Peromyscus*

Alternate food	No. of exp'ts	No. of cocoons opened	
		$\bar{X}$	S.E.$_{\bar{x}}$
none	7	165.9	11.4
dog biscuits	5	143.0	8.3
sunflower seeds	8	60.0	6.2
sunflower seeds and dog biscuits	8	21.5	4.2

an important effect, the consumption of cocoons by a caged *Peromyscus* was measured when no alternate foods, or one or two alternate foods, were present. Only female cocoons were used and these were provided at a density of 75 per sq. ft. to ensure that the level portion of the functional response would be measured. As in the previous experiments, the animal was familiarized with the experimental conditions and with cocoons for a preliminary two-week period. The average numbers of cocoons consumed each day with different numbers and kinds of alternate foods present are shown in Table III. This table again shows that fewer cocoons were consumed when sunflower seeds (high palatability) were present than when dog biscuits (low palatability) were present. In both cases, however, the consumption was lower than when no alternate foods were available. When two alternate foods were available, i.e., both sunflower seeds and dog biscuits, the consumption dropped even further. Thus, increase in both the palatability and in the number of different kinds of alternate foods decreases the functional response.

DISCUSSION

General

It has been argued that three of the variables affecting predation—characteristics of the prey, density and quality of alternate foods and characteristics of the predators — are subsidiary components of predation. The laboratory experiments showed that the functional response was lowered when the strength of stimulus, one prey characteristic, detected from cocoons was decreased or when the number of kinds and palatability of alternate foods was increased. Hence the effect of these subsidiary components is exerted through the functional response. Now the numerical response is closely related to the functional, since such an increase in predator density depends upon the amount of food consumed. It follows, therefore, that the subsidiary components will also affect the numerical response. Thus when the functional response is lowered by a decrease in the strength of stimulus detected from prey, the numerical response similarly must be decreased and predation will be less as a result of decrease of the two basic responses.

The density and quality of alternate foods could also affect the numerical response. Returning to the numerical responses shown in Fig. 3, if increase in the density or quality of alternate foods involved solely increase in food "per se", then the number of mammals would reach a maximum at a lower cocoon density, but the maximum itself would not change. If increase in alternate foods also involved changes in the agents limiting the numerical responses

(e.g. increased cover and depth of humus), then the maximum density the small mammals could attain would increase. Thus increase in the amount of alternate foods could increase the density of predators.

Increase in alternate foods *decreases* predation by dilution of the functional response, but *increases* predation by promoting a favourable numerical response. The relative importance of each of these effects will depend upon the particular problem. Voûte (1946) has remarked that insect populations in cultivated woods show violent fluctuations, whereas in virgin forests or mixed woods, where the number of alternate foods is great, the populations are more stable. This stability might result from alternate foods promoting such a favourable numerical response that the decrease in the functional response is not great enough to lower predation.

The importance of alternate foods will be affected by that part of the third subsidiary component – characteristics of the predators – that concerns food preferences. Thus an increase in plants or animals other than the prey will most likely affect the responses of those predators, like the omnivore *Peromyscus*, that are not extreme food specialists. Predation by the more stenophagous shrews, would only be affected by some alternate, animal food.

Food preferences, however, are only one of the characteristics of predators. Others involve their ability to detect, capture, and kill prey. But again the effect of these predator characteristics will be exerted through the two basic responses, the functional and numerical. The differences observed between the functional responses of the three species shown earlier in Fig. 1 undoubtedly reflect differences in their abilities to detect, capture, and kill. The amount of predation will similarly be affected by the kind of sensory receptor, whether visual, olfactory, auditory, or tactile, that the predator uses in locating prey. An efficient nose, for example, is probably a less precise organ than an efficient eye. The source of an undisturbed olfactory stimulus can only be located by investigating a gradient in space, whereas a visual stimulus can be localized by an efficient eye from a single point in space – the telotaxis of Fraenkel and Gunn (1940). As N. Tinbergen (1951) remarked, localization of direction is developed to the highest degree in the eye. Thus the functional response of a predator which locates prey by sight will probably reach a maximum at a much lower prey density than the response of one that locates its prey by odour. In the data presented by Tothill (1922) and L. Tinbergen (1949), the per cent predation of insects by birds was highest at very low prey densities, suggesting that the functional responses of these "visual predators" did indeed reach a maximum at a low density.

The Effect of Predation on Prey Populations

One of the most important characteristics of mortality factors is their ability to regulate the numbers of an animal – to promote a "steady density" (Nicholson, 1933; Nicholson and Bailey, 1935) such that a continued increase or decrease of numbers from this steady state becames progressively unlikely the greater the departure from it. Regulation in this sense therefore requires that the mortality factor change with change in the density of the animal attacked, i.e. it requires a direct density-dependent mortality (Smith, 1935, 1939). Density-independent factors can affect the numbers of an animal but alone they cannot *regulate* the numbers. There is abundant evidence that changes in climate, some aspects of which are presumed to have a density-independent action, can lower or raise the numbers of an animal. But this need not be regulation. Regulation will only result from an interaction with a density-dependent factor, an interaction

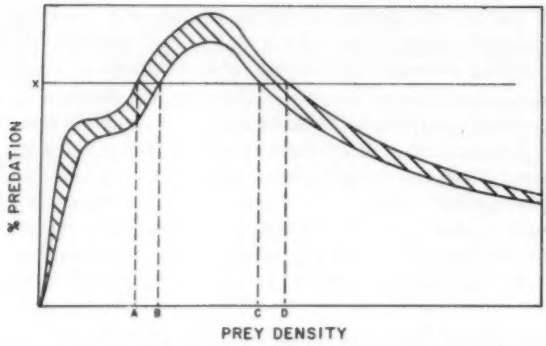

Fig. 7. Theoretical model showing regulation of prey by predators. (see text for explanation).

that might be the simplest, i.e. merely additive. Recently, the density-dependent concept has been severely criticized by Andrewartha and Birch (1954). They call it a dogma, but such a comment is only a criticism of an author's use of the concept. Its misuse as a dogma does not militate against its value as a hypothesis.

We have seen from this study that predation by small mammals does change with changes in prey density. As a result of the functional and numerical responses the proportion of prey destroyed increases from zero to some finite prey density and thereafter decreases. Thus predation over some ranges of prey density shows a direct density-dependent action. This is all that is required for a factor to regulate.

The way in which predation of the type shown in this study can regulate the numbers of a prey species can best be shown by a hypothetical example. To simplify this example we will assume that the prey has a constant rate of reproduction over all ranges of its density, and that only predators are affecting its numbers. Such a situation is, of course, unrealistic. The rate of reproduction of real animals probably is low at low densities when there is slight possibility for contact between individuals (e.g. between male and female). It would rise as contacts became more frequent and would decline again at higher densities when the environment became contaminated, when intraspecific stress symptoms appeared, or when cannibalism became common. Such changes in the rate of reproduction have been shown for experimental populations of *Tribolium confusum* (MacLagan, 1932) and *Drosophila* (Robertson and Sang, 1944). Introducing more complex assumptions, however, confuses interpretations without greatly changing the conclusions.

This hypothetical model is shown in Fig. 7. The curve that describes the changes in predation with changes in prey density is taken from the actual data shown earlier in Fig. 4. It is assumed that the birth-rate of the prey at any density can be balanced by a fixed per cent predation, and that the variation in the environment causes a variation in the predation at any one density. The per cent predation necessary to balance the birth-rate is represented by the horizontal line, x%, in the diagram and variation in predation is represented by the thickness of the mortality curve. The death-rate will equal the birth-rate at two density ranges, between A and B and between C and D. When the densities of the prey are below A, the mortality will be lower than that necessary to balance

reproduction and the population will increase. When the densities of the animal are between B and C, death-rate will exceed birth-rate and the populations will decrease. Thus, the density of the prey will tend to fluctuate between densities A and B. If the density happens to exceed D, death-rate will be lower than birth-rate and the prey will increase in numbers, having "escaped" the control exerted by predators. This would occur when the prey had such a high rate of reproduction that its density could jump, in one generation, from a density lower than A to a density higher than D. If densities A and D were far apart, there would be less chance of this occurring. This spread is in part determined by the number of different species of predators that are present. Predation by each species peaks at a different density (see Fig. 4), so that increase in the number of species of predator will increase the spread of the total predation. This will produce a more stable situation where the prey will have less chance to escape control by predators.

Predation of the type shown will regulate the numbers of an animal whenever the predation rises high enough to equal the effective birth-rate. When the prey is an insect and predators are small mammals, as in this case, the reproductive rate of the prey will be too high for predation *alone* to regulate. But if other mortality occurs, density-independent or density-dependent, the total mortality could rise to the point where small mammals were contributing, completely or partially, to the regulation of the insect.

Predation of the type shown will produce stability if there are large numbers of different species of predators operating. Large numbers of such species would most likely occur in a varied environment, such as mixed woods. Perhaps this explains, in part, Voûte's (1946) observation that insect populations in mixed woods are less liable to show violent fluctuations.

I cannot agree with Voûte (1956 and 1958) that factors causing a peaked mortality curve are not sufficient for regulation. He states (1956) that "this is due to the fact that mortality only at low densities increases with the increase of the population. At higher densities, mortality decreases again. The growth of the population is at the utmost slowed down, never stopped". All that is necessary for regulation, however, is a rise in per cent predation over some range of prey densities and an *effective* birth-rate that can be matched at some density by mortality from predators.

Neither can I agree with Thompson (1930) when he ascribes a minor role to vertebrate predators of insects and states that "the number of individuals of any given species (i.e. of vertebrate predators) is . . . relatively small in comparison with those of insects and there is no reason to suppose that it varies primarily in function of the supply of insect food, which fluctuates so rapidly that it is impossible for vertebrates to profit by a temporary abundance of it excepting to a very limited extent". We know that they do respond by an increase in numbers and even if this is not great in comparison with the numerical response of parasitic flies, the number of prey killed per predator is so great and the increase in number killed with increase in prey density is so marked as to result in a heavy proportion of prey destroyed; a proportion that, furthermore, increases initially with increase of prey density. Thompson depreciates the importance of the numerical response of predators and ignores the functional response.

In entomological literature there are two contrasting mathematical theories of regulation. Each theory is based on different assumptions and the predicted results are quite different. Both theories were developed to predict the inter-

action between parasitic flies and their insect hosts but they can be applied equally well to predator-prey relations. Thompson (1939) assumes that a predator has a limited appetite and that it has no difficulty in finding its prey. Nicholson (1933) assumes that predators have insatiable appetites and that they have a specific capacity to find their prey. This searching capacity is assumed to remain constant at all prey densities and it is also assumed that the searching is random.

The validity of these mathematical models depends upon how closely their assumptions fit natural conditions. We have seen that the appetites of small mammal predators in this study are not insatiable. This fits one of Thompson's assumptions but not Nicholson's. When the functional response was described, it was obvious that predators did have difficulty in finding their prey and that their searching ability did not remain constant at all prey densities. Searching by small mammals was not random. Hence in the present study of predator-prey relations, the remaining assumptions of both Thompson and Nicholson do not hold.

Klomp (1956) considers the damping of oscillations of animal numbers to be as important as regulation. If the oscillations of the numbers of an animal affected by a delayed density-dependent factor (Varley, 1947) like a parasite, do increase in amplitude, as Nicholson's theory predicts (Nicholson and Bailey, 1935), then damping is certainly important. It is not at all certain, however, that this prediction is true. We have already seen that the assumptions underlying Nicholson's theory do not hold in at least some cases. In particular he ignores the important possibility of an S-shaped functional response of the type shown by small mammal predators. If the parasites did show an S-shaped functional response, there would be an *immediate* increase in per cent predation when host density increased, an increase that would modify the effects of the delayed numerical response of parasites emphasized by Nicholson and Varley. Under these conditions the amplitude of the oscillations would not increase as rapidly, and might well not increase at all. An S-shaped functional response therefore acts as an intrinsic damping mechanism in population fluctuations.

Oscillations undoubtedly do occur, however, and whether they increase in amplitude or not, any extrinsic damping is important. The factor that damps oscillations most effectively will be a concurrent density-dependent factor that reacts immediately to changes in the numbers of an animal. Predation by small mammals fulfils these requirements when the density of prey is low. The consumption of prey by individual predators responds immediately to increase in prey density (functional response). Similarly, the numerical response is not greatly delayed, probably because of the high reproductive capacity of small mammals. Thus if the density of a prey is low, chance increases in its numbers will immediately increase the per cent mortality caused by small mammal predation. When the numbers of the prey decrease, the effect of predation will be immediately relaxed. Thus, incipient oscillations can be damped by small-mammal predation.

We have seen that small mammals theoretically can regulate the numbers of prey and can damp their oscillations under certain conditions. Insufficient information was obtained to assess precisely the role of small mammals as predators of *N. sertifer* in the pine plantations of southwestern Ontario, however. Before the general introduction of a virus disease in 1952 (Bird, 1952, 1953), the sawfly was exhausting its food supplies and 70 to 100% defoliation of Scots, jack and red pines was observed in this area. Predators were obviously not regulating

the numbers of the sawfly. After the virus was introduced, however, sawfly populations declined rapidly. In Plot 1, for example, their numbers declined from 248,000 cocoons per acre in 1952 to 39,000 per acre in 1954. The area was revisited in 1955 and larval and cocoon population had obviously increased in this plot, before the virus disease could cause much mortality. It happened, however, that *Peromyscus* was the only species of small mammal residing in Plot 1 and it is interesting that similar increases were not observed in other plantations where sawfly numbers had either not decreased so greatly, or where shrews, the most efficient predators, were present. These observations suggest that predation by shrews was effectively damping the oscillations resulting from the interaction of the virus disease with its host.

Types of Predation

Many types of predation have been reported in the literature. Ricker (1954) believed that there were three major types of predator-prey relations, Leopold (1933) four, and Errington (1946, 1956) two. Many of these types are merely minor deviations, but the two types of predation Errington discusses are quite different from each other. He distinguishes between "compensatory" and "noncompensatory" predation. In the former type, predators take a heavy toll of individuals of the prey species when the density of prey exceeds a certain threshold. This "threshold of security" is determined largely by the number of secure habitable niches in the environment. When prey densities become too high some individuals are forced into exposed areas where they are readily captured by predators. In this type of predation, predators merely remove surplus animals, ones that would succumb even in the absence of enemies. Errington feels, however, that some predator-prey relations depart from this scheme, so that predation occurs not only *above* a specific threshold density of prey. These departures are ascribed largely to behaviour characteristics of the predators. For example, he does not believe that predation of ungulates by canids is compensatory and feels that this results from intelligent, selective searching by the predators.

If the scheme of predation presented here is to fulfill its purpose it must be able to explain these different types of predation. Non-compensatory predation is easily described by the normal functional and numerical responses, for predation of *N. sertifer* by small mammals is of this type. Compensatory predation can also be described using the basic responses and subsidiary factors previously demonstrated. The main characteristic of this predation is the "threshold of security". Prey are more vulnerable above and less vulnerable below this threshold. That is, the strength of stimulus perceived from prey increases markedly when the prey density exceeds the threshold. We have seen from the present study that an increase in the strength of stimulus from prey increases both the functional and numerical responses. Therefore, below the "threshold of security" the functional responses of predators will be very low and as a result there will probably be no numerical response. Above the threshold, the functional response will become marked and a positive numerical response could easily occur. The net effect will result from a combination of these functional and numerical responses so that per cent predation will remain low so long as there is sufficient cover and food available for the prey. As soon as these supply factors are approaching exhaustion the per cent predation will suddenly increase.

Compensatory predation will occur (1) when the prey has a specific density level near which it normally operates, and (2) when the strength of stimulus perceived by predators is so low below this level and so high above it that there

is a marked change in the functional response. Most insect populations tolerate considerable crowding and the only threshold would be set by food limitations. In addition, their strength of stimulus is often high at all densities. For *N. sertifer* at least, the strength of stimulus from cocoons is great and the threshold occurs at such high densities that the functional responses of small mammals are at their maximum. Compensatory predation upon insects is probably uncommon.

Entomologists studying the biological control of insects have largely concentrated their attention on a special type of predator – parasitic insects. Although certain features of a true predator do differ from those of a parasite, both predation and parasitism are similar in that one animal is seeking out another. If insect parasitism can in fact be treated as a type of predation, the two basic responses to prey (or host) density and the subsidiary factors affecting these responses should describe parasitism. The functional response of a true predator is measured by the number of prey it destroys; of a parasite by the number of hosts in which eggs are laid. The differences observed between the functional responses of predators and parasites will depend upon the differences between the behaviour of eating and the behaviour of egg laying. The securing of food by an individual predator serves to maintain that individual's existence. The laying of eggs by a parasite serves to maintain its progenies' existence. It seems likely that the more a behaviour concerns the maintenance of an individual, the more demanding it is. Thus the restraints on egg laying could exert a greater and more prolonged effect than the restraints on eating. This must produce differences between the functional responses of predators and parasites. But the functional responses of both are similar in that there is an upper limit marked by the point at which the predator becomes satiated and the parasite has laid all its eggs. This maximum is reached at some finite prey or host density above zero. The form of the rising phase of the functional response would depend upon the characteristics of the individual parasite and we might expect some of the same forms that will be postulated for predators at the end of this section. To summarize, I do not wish to imply that the characteristics of the functional response of a parasite are identical with those of a predator. I merely wish to indicate that a parasite has a response to prey density – the laying of eggs – that can be identified as a functional response, the precise characteristics of which are unspecified.

The effects of host density upon the number of hosts parasitized have been studied experimentally by a number of workers (e.g., Ullyett, 1949a and b; Burnett, 1951 and 1954; De Bach and Smith, 1941). In each case the number of hosts attacked per parasite increased rapidly with initial increase in host density but tended to level with further increase. Hence these functional response curves showed a continually decreasing slope as host density increased and gave no indication of the S-shaped response shown by small mammals. Further information is necessary, however, before these differences can be ascribed solely to the difference between parasitism and predation. It might well reflect, for example, a difference between an instinctive response of an insect and a learned response of a mammal or between the absence of an alternate host and the presence of an alternate food.

The numerical response of both predators and parasites is measured by the way in which the number of adults increases with increase in prey or host density. At first thought, the numerical response of a parasite would seem to be so intimately connected with its functional response that they could not be separated. But the two responses of a predator are just as intimately connected.

The predator must consume food in order to produce progeny just as the parasite must lay eggs in order to produce progeny.

The agents limiting the numerical response of parasites will be similar to those limiting the response of predators. There is, however, some difference. During at least one stage of the parasites' life, the requirements for both food and niche are met by the same object. Thus increase in the amount of food means increase in the number of niches as well, so that niches are never limited unless food is. This should increase the chances for parasites to show pronounced numerical responses. The characteristics of the numerical responses of both predators and parasites, however, will be similar and will range from those in which there is no increase with increase in the density of hosts, to those in which there is a marked and prolonged increase.

A similar scheme has been mentioned by Ullyett (1949b) to describe parasitism. He believed that "the problem of parasite efficiency would appear to be divided into two main phases, viz.: (a) the efficiency of the parasite as a mortality factor in the host population, (b) its efficiency as related to the maintenance of its own population level within the given area". His first phase resembles the functional response and the second the numerical response. Both phases or responses will be affected, of course, by subsidiary components similar to those proposed for predation—characteristics of the hosts, density and quality of alternate hosts, and characteristics of the parasite. The combination of the two responses will determine the changes in per cent parasitism as the result of changes in host density. Since both the functional and numerical responses presumably level at some point, per cent parasitism curves might easily be peaked, as were the predation curves. If these responses levelled at a host density that would never occur in nature, however, the decline of per cent parasitism might never be observed.

The scheme of predation revealed in this study may well explain all types of predation as well as insect parasitism. The knowledge of the basic components and subsidiary factors underlying the behaviour permits us to imagine innumerable possible variations. In a hypothetical situation, for example, we could introduce and remove alternate food at a specific time in relation to the appearance of a prey, and predict the type of predation. But such variations are only minor deviations of a basic pattern. The major types of predation will result from major differences in the form of the functional and numerical responses.

If the functional responses of some predators are partly determined by their behaviour, we could expect a variety of responses differing in form, rate of rise, and final level reached. All functional responses, however, will ultimately level, for it is difficult to imagine an individual predator whose consumption rises indefinitely. Subsistence requirements will fix the ultimate level for most predators, but even those whose consumption is less rigidly determined by subsistence requirements (e.g., fish, Ricker 1941) must have an upper limit, even if it is only determined by the time required to kill.

The functional responses could conceivably have three basic forms. The mathematically simplest would be shown by a predator whose pattern of searching was random and whose rate of searching remained constant at all prey densities. The number of prey killed per predator would be directly proportional to prey density, so that the rising phase would be a straight line. Ricker (1941) postulated this type of response for certain fish preying on sockeye salmon, and De Bach and Smith (1941) observed that the parasitic fly, *Muscidifurax raptor*,

parasitized puparia of *Musca domestica*, provided at different densities, in a similar fashion. So few prey were provided in the latter experiment, however, that the initial linear rise in the number of prey attacked with increase in prey density may have been an artifact of the method.

A more complex form of functional response has been demonstrated in laboratory experiments by De Bach and Smith (1941), Ullyett (1949a) and Burnett (1951, 1956) for a number of insect parasites. In each case the number of prey attacked per predator increased very rapidly with initial increase in prey density, and thereafter increased more slowly approaching a certain fixed level. The rates of searching therefore became progressively less as prey density increased.

The third and final form of functional response has been demonstrated for small mammals in this study. These functional responses are S-shaped so that the rates of searching at first increase with increase of prey density, and then decrease.

Numerical responses will also differ, depending upon the species of predator and the area in which it lives. Two types have been demonstrated in this study. *Peromyscus* and *Sorex* populations, for example, increased with increase of prey density to the point where some agent or agents other than food limited their numbers. These can be termed direct numerical responses. There are some cases, however, where predator numbers are not affected by changes of prey density and in the plantations studied *Blarina* presents such an example of no numerical response. A final response, in addition to ones shown here, might also occur. Morris *et al.* (1958) have pointed out that certain predators might decrease in numbers as prey density increases through competition with other predators. As an example of such inverse numerical responses, he shows that during a recent outbreak of spruce budworm in New Brunswick the magnolia, myrtle, and black-throated green warblers decreased in numbers. Thus we have three possible numerical responses – a direct response, no response, and an inverse response.

The different characteristics of these types of functional and numerical responses produce different types of predation. There are four major types conceivable; these are shown diagramatically in Fig. 8. Each type includes the three possible numerical responses – a direct response (a), no response (b), and an inverse response (c), and the types differ because of basic differences in the functional response. In type 1 the number of prey consumed per predator is assumed to be directly proportional to prey density, so that the rising phase of the functional response is a straight line. In type 2, the functional response is presumed to rise at a continually decreasing rate. In type 3, the form of the functional response is the same as that observed in this study. These three types of predation may be considered as the basic ones, for changes in the subsidiary components are not involved. Subsidiary components can, however, vary in response to changes of prey density and in such cases the basic types of predation are modified. The commonest modification seems to be Errington's compensatory predation which is presented as Type 4 in Fig. 8. In this figure the vertical dotted line represents the "threshold of security" below which the strength of stimulus from prey is low and above which it is high. The functional response curves at these two strengths of stimulus are given the form of the functional responses observed in this study. The forms of the responses shown in Types 1 and 2 could also be used, of course.

The combination of the two responses gives the total response shown in the

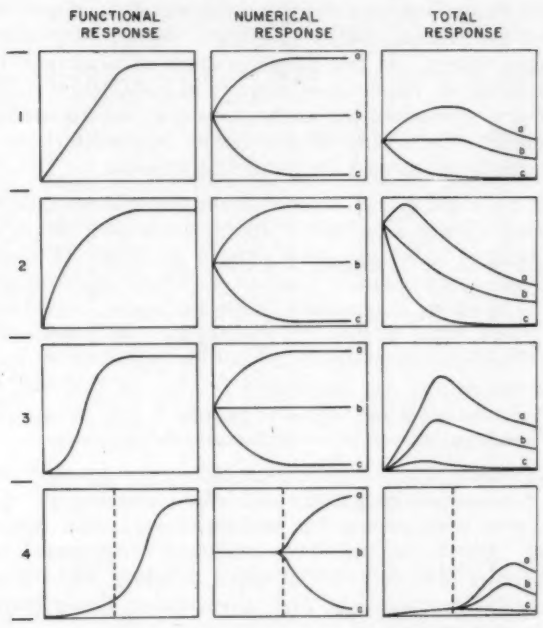

Fig. 8. Major types of predation.

final column of graphs of Fig. 8. Both peaked (curves 1a; 2a; 3a, b, c; 4a, b, c) and declining (1b, c; 2b, c) types of predation can occur, but in the absence of any other density-dependent factor, regulation is possible only in the former type.

This method of presenting the major types of predation is an oversimplification since predator density is portrayed as being directly related to prey density. Animal populations, however, cannot respond *immediately* to changes in prey density, so that there must be a delay of the numerical response. Varley (1953) pointed this out when he contrasted "delayed density dependence" and "density dependence". The degree of delay, however, will vary widely depending upon the rate of reproduction, immigration, and mortality. Small mammals, with their high reproductive rate, responded so quickly to increased food that the delay was not apparent. In such cases the numerical response graphs of Fig. 8 are sufficiently accurate, for the density of predators in any year is directly related to the density of prey in the same year. The numerical response of other natural enemies can be considerably delayed, however. Thus the density of those insect parasites that have one generation a year and a low rate of immigration results from the density of hosts in the preceding generation.

In these extreme cases of delay the total response obtained while prey or hosts are steadily increasing will be different than when they are steadily decreasing. The amount of difference will depend upon the magnitude and amount of delay of the numerical response, for the functional response has no element of delay.

SUMMARY AND CONCLUSIONS

The simplest and most basic type of predation is affected by only two variables – prey and predator density. Predation of cocooned *N. sertifer* by small

mammals is such a type, for prey characteristics, the number and variety of alternate foods, and predilections of the predators do not vary in the plantations where *N. sertifer* occurs. In this simple example of predation, the basic components of predation are responses to changes in prey density. The increase in the number of prey consumed per predator, as prey density rises, is termed the functional response. The change in the density of predators, as a result of increase in prey density, is termed the numerical response.

The three important species of small mammal predators (*Blarina*, *Sorex*, and *Peromyscus*) each showed a functional response, and each curve, whether it was derived from field or laboratory data, showed an initial S-shaped rise up to a constant, maximum consumption. The rate of increase of consumption decreased from *Blarina* to *Sorex* to *Peromyscus*, while the upper, constant level of consumption decreased from *Blarina* to *Peromyscus* to *Sorex*. The characteristics of these functional responses could not be explained by a simple relation between consumption and the proportion of prey in the total food available. The form of the functional response curves is such that the proportion of prey consumed per predator increases to a peak and then decreases.

This peaked curve was further emphasized by the direct numerical response of *Sorex* and *Peromyscus*, since their populations rose initially with increase in prey density up to a maximum that was maintained with further increase in cocoon density. *Blarina* did not show a numerical response. The increase in density of predators resulted from increased breeding, and because the reproductive rate of small mammals is so high, there was an almost immediate increase in density with increase in food.

The two basic components of predation – the functional and numerical responses – can be affected by a number of subsidiary components: prey characteristics, the density and quality of alternate foods, and characteristics of the predators. It was shown experimentally that these components affected the amount of predation by lowering or raising the functional and numerical responses. Decrease of the strength of stimulus from prey, one prey characteristic, lowered both the functional and numerical responses. On the other hand, the quality of alternate foods affected the two responses differently. Increase in the palatability or in the number of kinds of alternate foods lowered the functional response but promoted a more pronounced numerical response.

The peaked type of predation shown by small mammals can theoretically regulate the numbers of its prey if predation is high enough to match the effective reproduction by prey at some prey density. Even if this condition does not hold, however, oscillations of prey numbers are damped. Since the functional and numerical responses undoubtedly differ for different species of predator, predation by each is likely to peak at a different prey density. Hence, when a large number of different species of predators are present the declining phase of predation is displaced to a higher prey density, so that the prey have less chance to "escape" the regulation exerted by predators.

The scheme of predation presented here is sufficient to explain all types of predation as well as insect parasitism. It permits us to postulate four major types of predation differing in the characteristics of their basic and subsidiary components.

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